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THE HORNWORM PARASITE, APANTELES CONGREGATUS SAY AND THE HYPERPARASITE, HYPOPTEROMALUS TABACUM (FITCH)[1]

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Apanteles congregatus Say

Apanteles congregatus (Say) is a common and widely distributed parasite of Sphingidae. In North Carolina it is the most important enemy of the catalpa sphinx, *Ceratomia catalpae* (Bdv.) and the tomato worm, *Protoparce sexta* (Johan.), which in this region is usually called the tobacco hornworm. The hornworms increase in numbers rapidly in the late summer in fields where the tobacco stalks are left standing after harvest, and if the foliage is not completely destroyed they will usually remain in the fields until the first killing frost. Hornworm eggs can often be found in the field as late as October 1. The percentage of hornworms parasitized by Apanteles also increases steadily but there is considerable variation between different fields. Some records were taken of the number of hornworms with and without Apanteles cocoons on different dates in the same field as follows:

Aug. 11, 1936—	Total worms counted			100.	With cocoons		0%
Sept. 15, 1936	"	"	"	116.	"	"	16.6%
Sept. 28, 1936	"	"	"	32.	"	"	34.3%

On the last date most of the stalks had been cut recently so that the number of worms was reduced. In another field about two miles away there were 70% of the hornworms with cocoons out of a total of 150 counted.

In the following year another tobacco field was selected for similar records which were as follows:

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[1]Contribution from the Department of Zoology and Entomology, North Carolina State College, published with the approval of the Director of the North Carolina Experiment Station as paper no. 112 of the Journal Series.

Aug. 26, 1937—	Total worms counted			53.	With cocoons		1.9%
Sept. 9, 1937	"	"	"	90.	"	"	22.2%
Sept. 16, 1937	"	"	"	80.	"	"	36.2%
Sept. 24, 1937	"	"	"	80.	"	"	31.2%
Sept. 30, 1937	"	"	"	80.	"	"	45.0%
Oct. 7, 1937	"	"	"	62.	"	"	82.2%
Oct. 15, 1937	Worms killed by frost.						

A high percentage of parasitism by Apanteles may occur earlier as shown by a record taken Aug. 25, 1938, in a tobacco field where 32.8% of the hornworms had cocoons out of a total of 149 counted.

The percentage of parasitized hornworms is probably considerably higher than the percentage of those bearing cocoons. When nearly half of the worms show cocoons it is difficult to find a worm that does not contain Apanteles larvae. On the other hand, parasitized worms remain on the plants longer and those with the white cocoons are easier to find than the normal hornworms.

A number of hyperparasites have been reared from the cocoons of *Apanteles congregatus*. The proportion and species of hyperparasites emerging varies with place and time. Only two species have so far been found to be important parasites of *Apanteles congregatus* on the two host caterpillars studied in the vicinity of Raleigh, N. C. Of these, *Horismanus floridanus* (Ashm.) has been the most common in the smaller number of collections of Apanteles cocoons from the catalpa sphinx. *Hypopteromalus tabacum* (Fitch) is the most important when the Apanteles host is a hornworm either on tobacco or tomato, and it is also a common hyperparasite of the catalpa sphinx. Some of the collections in which the species reared have been identified by specialists at the U. S. National Museum are given in Table I.

OVIPOSITION

Apanteles congregatus adults have been observed flying in tobacco fields. They have a darting, zigzag flight and occasionally stop to rest on a tobacco leaf. Sometimes several can be seen hovering around a single plant. One plant having two small hornworms about an inch long and two large ones about two inches long was watched for half an hour. During that time a number of Apanteles were observed hovering near the hornworms and sometimes one would alight on a worm from flight. More often the Apanteles would land on a leaf near the worm, approach cautiously, and suddenly jump on the worm from the leaf. The posterior part of the worm is the favorite point of attack and the worm immediately lashes its head about to drive the wasp away, so that the wasp is seldom on the worm more than a few seconds. The small worms were more often attacked than the larger worms.

As it was impossible to determine in the field whether the oviposition was accomplished in the brief time the wasps remained on the worms, *Apanteles* adults were confined with small worms reared from the eggs in petri dishes. The wasps were observed clinging to the worms never more than a few seconds before being shaken off. After a few hours some of the worms were opened and a large number of Apanteles eggs were found. Later a single hornworm larva reared from the egg was

placed in a dish with Apanteles and kept under continuous observation. After six Apanteles had landed on the worm for a duration of about

TABLE I

PERCENTAGE AND SPECIES OF HYPERPARASITES ON DIFFERENT DATES AND HOSTS AT FIVE COLLECTING STATIONS NEAR RALEIGH, N. C.

Date Collected	Host and Food Plant	Collecting Station	Total Emergence	Percent Hyperparasites	Species of Hyperparasites[2]
Aug. 17, 1937	*Protoparce sexta* tomato	1 (Raleigh)	317	39	*Hypopteromalus tabacum* (Fitch)
Aug. 24, 1937	*P. sexta* tomato	2 (1 mile west of 1)	534	0	
Sept. 2, 1937	*Ceratomia catalpae* catalpa	1	249	0	*Hypopteromalus tabacum* *Horismenus floridanus* (Ashm.) *Acrolyta mesochori* Ashm.
Sept. 8, 1937	*P. sexta* tomato	3 (½ mile north of 1)	512	0	
Sept. 9, 1937	*P. sexta* tobacco	4 (12 miles west of 1)	419	3	*Spilochalcis side* (Walk.) *Ceratosmicra* n. sp.
Sept. 14, 1937	*Ceratomia catalpae* catalpa	3	429	61	*Horismenus floridanus*
Sept. 16, 1937	*P. sexta* tobacco	4	218	5	*Spilochalcis side* *Ceratosmicra* n. sp.
Sept. 17, 1937	*P. sexta* tomato	3	893	19	*Hypopteromalus tabacum*
Sept. 17, 1937	*P. sexta* tomato	2	570	53	*Hypopteromalus tabacum*
Sept. 20, 1937	*P. sexta* tobacco	5 (2 miles south of 4)	187	75	*Hypopteromalus tabacum*
Sept. 24, 1937	*P. sexta* tobacco	4	307	100	*Hypopteromalus tabacum*

[2]Species determinations by C. F. W. Muesebeck, R. A. Cushman, and A. B. Gahan.

one or two seconds each, the worm was removed and opened under water. After scraping the skin with a scalpel, 122 eggs were found.

Another hornworm was kept under observation until only one Apanteles had attacked. This one appeared to have the ovipositor in the worm for a few seconds. The point of attack was marked and a piece of skin a few millimeters square was removed at that point. This was scraped under water and 28 eggs were found.

The Apanteles ovipositor is about .5 mm. long. It tapers from a heavy base, about .1 mm. in diameter to a diameter of .03 at the middle, beyond which the thickness is more nearly uniform. At the middle the outside diameter is slightly less than that of the newly deposited egg. Since the lumen at the middle appears to have a diameter only about half as great as the outside diameter, the egg must be subjected to considerable distortion in its passage through the ovipositor. In spite of this the female Apanteles is able to deposit a large number of eggs in a very brief space of time.

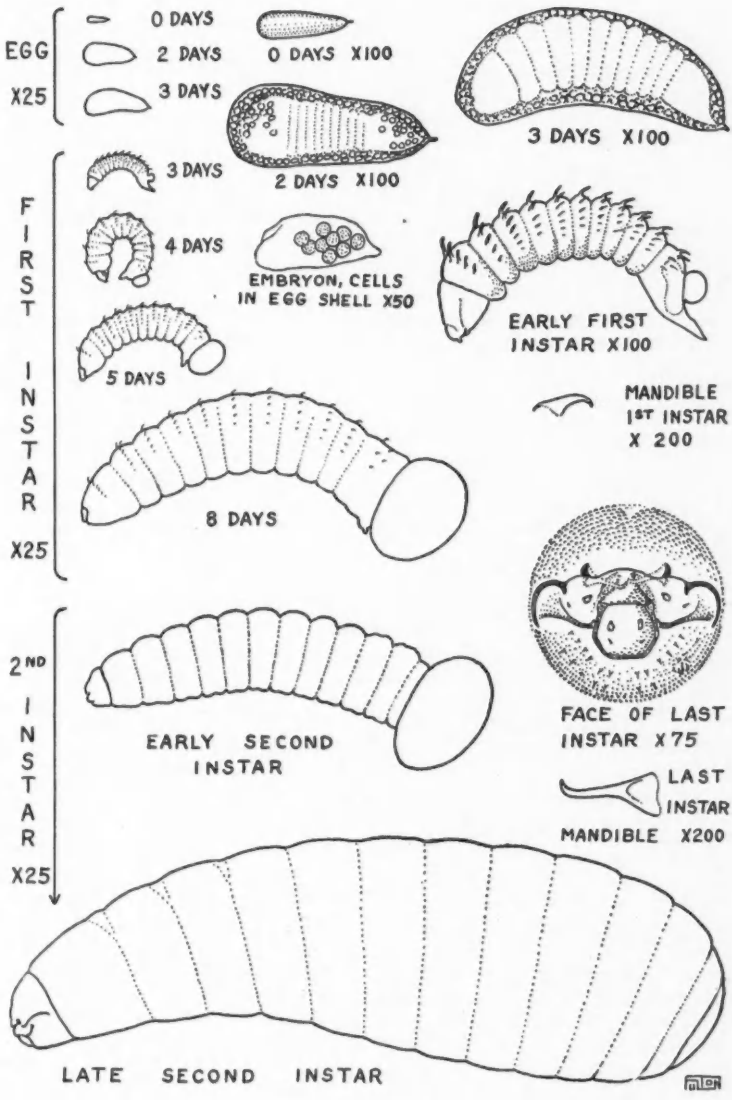
From examination of hornworms collected in the field it would appear that most of the eggs are deposited in first or second instar worms. Eggs and sometimes small larvae are found in many first instar worms. The second instar worms usually contained both eggs and larvae but some had only small larvae. Third instar worms usually contained larvae only but in a few eggs could also be found. Most of the fourth instar hornworms examined contained first instar Apanteles, but some contained second instar Apanteles, and frequently they are found emerging from fourth instar hornworms. A few fifth instar hormworms were found containing first instar Apanteles.

EGG

The newly deposited eggs are white and thin walled. They are wedge-shaped but rounded at both ends. They measure .12 to .16 mm. in length by .04 mm. in diameter at the broad end. The small end bears a minute nipple-shaped protuberance.

Hornworms that had been exposed to oviposition by Apanteles were placed in an incubator at 29° to 30° C. One was opened the following day and the eggs were found to have increased greatly in size, measuring .26 to .37 mm. in length by .08 to .12 mm. in diameter. A hornworm opened on the second day contained eggs of about the same size, measuring .30 to .34 mm. by .13 to .14 mm. The embryo was distinctly visible with nine narrow segments in the middle portion of the body. It was surrounded by a layer of large spherical cells. The eggs showed considerable diversity in shape, some being broadly oval and others more elongated, either straight or curved. On the third day young larvae were found moving about and also eggs containing fully formed larvae. These eggs measured about .40 by .14 mm. Judging by the advance size of the eggs in the first larva opened it seems probable that some eggs must hatch on the second day after oviposition, at this temperature.

The cells surrounding the embryo increase in size as the embryo develops. A hatched egg was found which contained a number of cells of similar appearance but greatly increased in size, measuring .04 mm. in diameter, so that only three of them could lie side by side across the



Eggs and larvae of *Apanteles congregatus*, with age in days from time of oviposition.

diameter of the egg shell. In parasitized hornworms large numbers of cells of similar size and appearance may be found free in the blood. Free embryonic cells have been found in the host blood in the case of other parasites and it appears that they may constitute part of the food of the parasite. A full discussion and a review of the literature on these cells has been given by Vance (1).

FIRST INSTAR LARVA

The young larvae live free in the body cavity near the periphery and are more numerous in the posterior part. The smallest measured .4 or .5 mm. in length when extended. They have a short caudal appendage and a small caudal vesicle. There are eleven body segments each of which bears a transverse dorsal row of curved bristles. On the head there is a distinct labrum with a pair of short processes. The curved mandibles measure about .04 mm. in length.

A hornworm from the 29°–30° C. incubator opened on the fourth day after oviposition contained larvae about .75 mm. in length. On the fifth day larvae were 1.1 mm. long and on the eighth day two hornworms opened had larvae respectively about 1.3 mm. and 2.4 mm. long. The latter had the outer cuticle separated preparatory to molting. Assuming three days for incubation these larvae would have spent about five days in the first instar. The hornworms were kept in the incubator in an effort to determine the rate of growth at a constant temperature, but evidently the condition of the host or other factors besides temperature influenced the rate of growth.

Although a fivefold increase in length is an extreme amount of growth for a single insect instar, there is no evidence to indicate any intervening ecdysis. As the body grows the head, jaws, and bristles remain of constant size. In the young larva the head is prominent but at the end of the stage it becomes a mere patch on the first body segment. The caudal appendage decreases in relative size until it becomes very inconspicuous, while the caudal vesicle continues to expand until it extends considerably beyond the sides of the body. The extreme growth of the first instar *Apanteles congregatus* is not greatly different from that found by Vance (1) in *Apanteles thompsoni* Lyle or by Tower (2) in *A. militaris* Walsh.

SECOND INSTAR LARVA

During the second instar the increase in length is from 2.4 mm. to 4.5 or 5. mm. The larva loses the curved bristles found in the first instar, and gains a small additional posterior segment, making twelve complete body segments. The integument is very thin, colorless, and has no sclerotized parts. There are paired swellings (maxillae) at the sides of the mouth and a median swelling representing the labium. As the larva approaches the end of the second instar the darkened sclerotized, mouth parts of the third instar become visible through the integument and a pair of mandibles are then evident lying in a deep transverse fold above the maxillae. The caudal vesicle remains larger

than the body and a thin collar-like structure surrounds its base. This appears to be the remains of the first cast skin which could not pass over the caudal vesicle.

Near the end of second instar the caudal vesicle is drawn into the body leaving an area surrounded by the twelfth segment which looks like a small terminal segment but is probably not a true segment. In preserved larvae at this age the old cuticle is clearly separated from the new cuticle. The larvae are now ready to leave the host. While working their way out of the host the heads of the Apanteles larvae can be seen through the integument of the host slowly nodding up and down. The movement evidently serves to wear away the tissues of the host. Under magnification the slender mandibles may be observed working in and out of the fold where they are concealed when at rest. The mandibles do not meet but when raised they can cut and tear by the movements of the head. The host integument is finally punctured and the larva forces its head through the opening. It can then be seen swallowing bubbles of air. As it works farther out it bends ventrally and the old cuticle splits on the dorsal side and slips away from the body. The head remains attached while the fore part of the body is free, and the withered cuticle is stretched across the bend like the string of a bow.

When most of the body is out the head is pulled free and the larva stands erect with the posterior end of the body held by the cast cuticle which evidently extends well into the body of the host, and effectively prevents a flow of blood from the host. If the exuviae are pulled out at this time or after the cocoons are formed large drops of greenish blood will flow from the openings. Without the presence of the exuviae the blood would probably force the larvae off the host or interfere with cocoon making.

The number of Apanteles larvae emerging from a single host varies from a few to over three hundred. Most of them come out of the host at the same time so that the back of the hornworm may be covered with cocoon spinning larvae. Rarely a few stragglers have been found to emerge on the following day. The dead or dying host usually contains a number of Apanteles larvae that never emerge.

The hornworms which had been parasitized in the laboratory all died before any Apanteles completed their growth and at a time when no more adults were available. As a substitute young hornworms 15 to 20 mm. long were collected in the field and placed in the incubator at 29° to 30° C. Several were examined at first and found to contain Apanteles in the first instar from .5 mm. to 1.5 mm. in length. Apanteles larvae emerged from these worms on the seventh, ninth, tenth and twelfth days. As part of this time was probably spent in the first instar in each case it may be assumed that the duration of the second instar at this temperature may be less than seven days. The host larvae were kept in petri dishes with tobacco leaves for food and did not do well under such conditions so that none of the results of rearing Apanteles under constant temperature can be considered very significant. Gilmore (3) records a minimum of five days from oviposition to emergence from host, a much faster rate of development than any found in the present work.

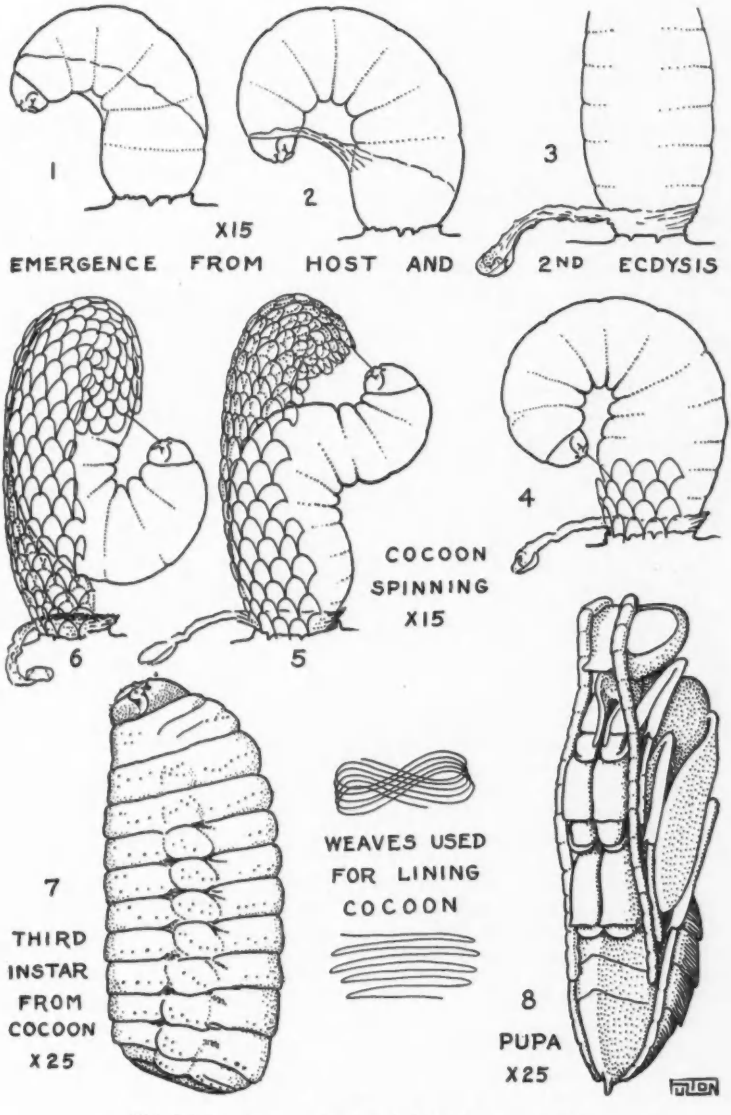
THIRD INSTAR LARVA

At the beginning of the third instar the larva is no different in appearance from the late second instar for all of its structures are plainly visible through the thin cuticle of that stage. It lacks the caudal vesicle and the integument is covered with very minute short spines and with a few scattered slightly larger spines in transverse rows on each segment. After the coccon is formed the body becomes considerably shorter.

Immediately after the second ecdysis and with the posterior end of the body still attached to the host, the larva begins to weave the cocoon, a process which has been correctly described by Cushman (4). The larva doubles up and attaches a thread to the host body close to the side of its own body. It pulls out a short length of silk and then attaches it again a little to one side, so that the thread forms a loop in the shape of an inverted "U." It continues in the same direction until it has formed a series of loops around the ventral half of its body. Some of them may be attached to the cast cuticle. Then it reverses the direction and attaches the loops to the tops of the first series. The last loop of each row is then attached to its own body until the frame work gets higher. This is very important to the success of the enterprise for a considerable pull is necessary to release the silk and if the frame becomes loosened it moves back and forth with the head and the silk fails to pull out properly. Even if it is rigid enough to draw the thread the frame may sag away from the body and develop as a long curved strip never reaching the proper height for completion.

When the larva has extended the frame up the ventral side of its body to its full height, it rounds off the top and by bending backward extends the frame downward in the form of a hood. It then crawls into the hood and reverses its direction so that large posterior portion of the body is held in the hood. Reaching back to where it left off it continues the looping process down the other side until the oval, basket-like frame is completed. Then it presses out the sides and spins a tight wall on the inside by alternating between two movements; first, back and forth straight longitudinal motions placing the threads in parallel series and second, transverse progressing loops like an elongated figure "8." Finally the cocoon is lined by a thin pellucid sheet composed of flattened strands running in various directions.

In building the cocoon the larva is guided by very rigid instincts and must follow a certain pattern. One larva which had built the original framework about half way up its body was subjected to an experiment. The whole framework including the strand at the mouth was suddenly removed while the larva was in the middle of a series of loops. Instead of going back to the beginning it continued at the same level going through the motions of completing the series of loops without drawing any silk until it reached the end of the row. Then it attached the silk to its body at that point and continued building the frame normally but with the bottom half missing. When the hood was completed, it crawled in, and fell off the host with it.



Third instar larva and pupa of *Apanteles congregatus*.

PUPA

During the summer the pupa is formed soon after the cocoon is completed. The cuticle of the third instar is pushed back to the end of the cocoon. At room temperature in September the period from formation of cocoons to emergence of adults was six or seven days. The only lot that emerged in the 30° C. incubator were found dead after six days and probably emerged nearer the third day when last examined. Gilmore (3) gives the period in the cocoon at Clarkville, Tennessee, in September as between six and eight days. The time spent in the pupa stage is probably not more than four or five days. Larvae cocooning a little before or after the first of October at Raleigh, remain over winter as larvae and pupate in the spring. One lot kept over winter in a screened insectary produced adults on April 5. In the field the cocoons remain on the host for some time but eventually fall to the ground or lodge in the axils of the tobacco leaves.

ADULT

The adults emerge from the cocoon by cutting off at one end a circular cap, which is pushed aside and usually remains attached. In the laboratory they lived only a few days, even when supplied with sugar water. Soon after emergence the males start mating. The males crawl toward the females fanning with their wings.

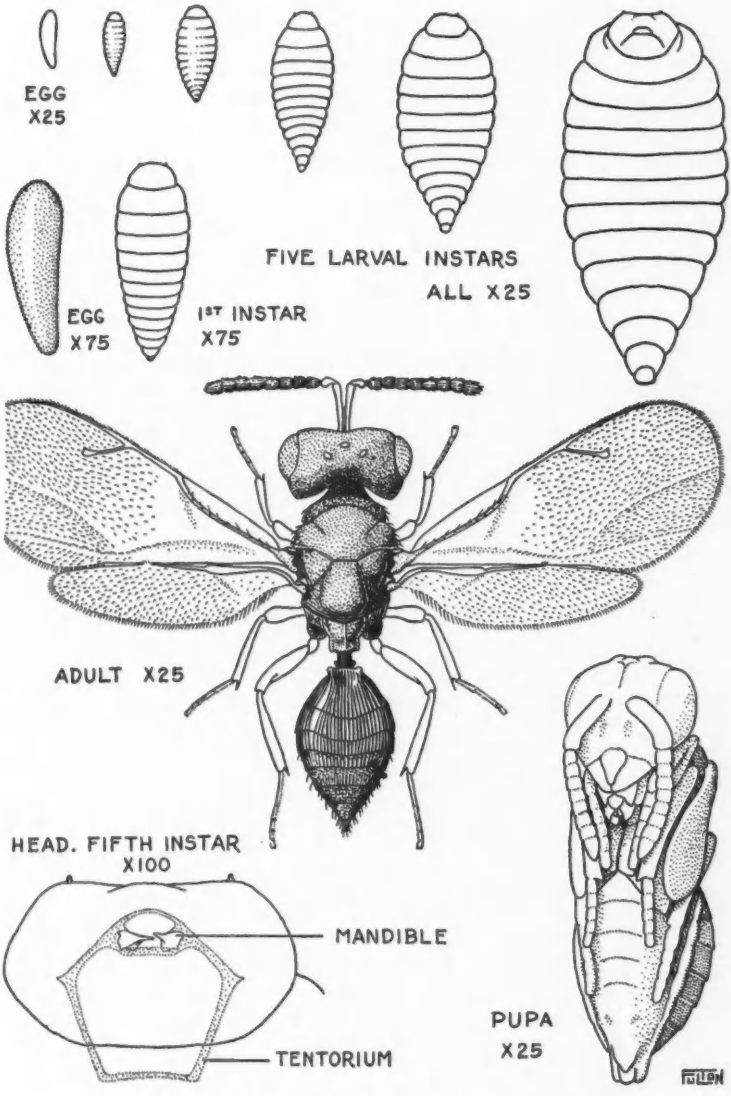
Data on the proportions of the sexes in lots from the same host indicate that the species is arrhenotokous. One lot of 58 produced 100% males, which may have been the progeny of a single unfertilized female. In all other lots the proportions varied from 8% to 50% males, and 37% for the total.

Hypopteromalus tabacum (Fitch)

Observation over the past three years indicate that *Hypopteromalus tobacum* is the most important enemy of *Apanteles congregatus* in the vicinity of Raleigh, N. C., especially when the host of the latter is the tobacco hornworm. The hyperparasite becomes abundant in autumn and adults can be found in the field after the adults of Apanteles have disappeared. The proportion of parasitized Apanteles continues to increase until cold weather prevents further reproduction. The date of the first killing frost should have considerable influence on the number of hibernating Apanteles. A prolonged growing season would tend to reduce the number and an early killing frost would have the opposite effect.

OVIPOSITION

In October adult Hypopteromalus may be frequently found in tobacco fields ovipositing in Apanteles cocoons, sometimes before the inner wall of the cocoon is completed. They are not easily disturbed and can be captured, without difficulty. In the laboratory they will continue to oviposit on loose cocoons in a vial or petri dish.



Egg, larva, pupa and adult female of *Hypopteromalus tabacum*.

In drilling into a cocoon the Chalcid first applies the tip of the abdomen to the cocoon and releases the ovipositor. Standing on the tips of her tarsi she pulls down hard with the legs while twisting the ovipositor. In one case a small particle of dried secretion on the side of the ovipositor could be observed making one complete revolution at each rotation of the ovipositor. In about one minute the cocoon is punctured and the ovipositor is inserted full length. The Chalcid then works it in and out and twists her body as if she were probing the inside of the cocoon. Apanteles larvae on which eggs are found appear to have been stung. The egg is deposited externally on the larva. More than one egg may be deposited on a single host, but two adults have not been reared from a single host. Eggs have not been found on pupae of Apanteles.

EGG

The egg of *Hypopteromalus* is much larger than the recently deposited Apanteles egg. It is white, elongated, with a greater curvature on one side and about twice as broad near one end as the other. The surface is uniformly studded with minute rounded knobs with intervening spaces several times their own diameter. The eggs vary in length from .28 to .36 mm. and in greatest diameter from .10 to .12 mm. The diameter of the shaft of the ovipositor is .03 mm. at the base and .025 mm. near the middle, with a lumen of about .01 mm. The egg therefore has a diameter 4 to 5 times that of the ovipositor and 10 to 12 times as great as the lumen through which it passes.

A number of Apanteles cocoons were exposed over night to oviposition by the chalcids. In the morning they were glued to cards and opened and those containing eggs were numbered and placed in a 30° C. incubator. By the next morning all had hatched and some of the larvae had apparently grown a little.

LARVA

The larva clings to the surface of the host and feeds externally. The newly hatched larva is between .3 and .4 mm. in length. It has thirteen body segments including a very small posterior one. The head is broad, semicircular in outline, with a pair of widely separated knob-like antennae on the anterior edge and with a pair of sickle-shaped mandibles and their supporting structures.

Measurements of a large number of head capsule diameters fall into five groups when plotted, indicating five larval instars. Head measurements in millimeters, for the different instars were as follows: first .09 to .12, second .14 to .16, third .19 to .23, fourth .27 to .30, fifth .40 to .46. There are no radical changes between instars. The bases of the mandibles become heavier, the supporting structures broader and the head gradually decreases in relative size and in the fifth instar shifts slightly toward the ventral side. The full grown larva is about 2.3 to 2.5 mm. long.

By the time the larva is full grown the host has been so completely devoured that it occupies very little space in the cocoon. The Chalcid larva then goes into a prepupal resting period during which the body undergoes some change in shape, and the contents of the alimentary tract are eliminated into the end of the cocoon.

In the 29° to 30° C. incubator the larvae grew very rapidly and approximately doubled in length each day. They were kept under daily observation in partially opened cocoons glued to a card. Of a number successfully reared from the egg, all had attained full growth, but not the prepupal condition on the third day after they were found hatched. Most of them had pupated by the fourth day, indicating that the prepupal period, found in some cases on the fourth day, must be considerably less than a day at that temperature.

PUPA

Out of nineteen larvae reared to the adult stage at 29° to 30° C., eight had matured by the fourth day after the pupa was found, ten by the fifth day and one by the sixth day. The average length of time in the pupa stage at this temperature must be about four and a half days. For about half of the period the pupa is pale colored, then the thorax darkens and finally the whole pupa becomes black.

ADULT

The entire developmental period from oviposition to emergence of the adult at 30° C. was either 9 or 10 days with a possible error of one day more or less. The adult chews a ragged edged hole in the cocoon by removing the wall in pieces. The hole is usually made in the side close to one end but sometimes directly in the end or nearer the middle. The adults cease to emerge about the first of October and go into hibernation even if kept in a warm place as is the case with Apanteles. In the laboratory they emerged in January or February but under natural conditions probably do not come out until spring. The stage in which hibernation is passed was not determined.

The adult has a bright metallic green head and thorax and pale yellowish brown legs and antennae. The abdomen of the female is nearly black with metallic green reflections. The abdomen of the male is dark brown with slightly greenish reflections on the posterior half and along the borders to the base, the anterior part being mainly yellowish brown.

The females feed on Apanteles blood through a tube formed by the ovipositor. The tube can be formed in about two minutes. After first inserting the ovipositor full length, it is almost entirely withdrawn, and slowly pushed in again while being worked up and down with a short stroke. At the same time an exudate appears on the lower part. After being pushed into the host again it is withdrawn leaving a portion of the exudate projecting as a short tube above the surface of the cocoon. After feeding at the tube for a time the female again inserts the ovipositor into the tube and works it around until the tube breaks off.

SUMMARY

Apanteles congregatus is a common parasite of Sphingidae and an important enemy of *Protoparce sexta*. The proportion of parasitized hornworms increases during autumn.

Apanteles deposits a large number of eggs in the host in a few seconds. The eggs increase greatly in size before hatching. There are two larval instars in the host. During the first instar the larvae increase fivefold in dimensions. The second instar larvae molt as they are leaving the host. The third instar larvae spin cocoons on the host. Until about October 1 the pupae are formed in a few days, after that time the larvae hibernate and pupate in the spring.

Several species of hyperparasites were reared from Apanteles cocoons. The most important enemy of Apanteles in tobacco fields is *Hypopteromalus tabacum* which may almost eliminate the primary parasite in certain fields in late fall. Its larvae feed externally on Apanteles larvae within the cocoons.

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ENVIRONMENTAL RESISTANCE[1] TO THE ESTABLISHMENT OF PARASITIC HYMENOPTERA[2]

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Before the establishment of an insect can take place, a complicated set of circumstances and conditions usually must exist (Smith *et al.*, 1933). As pointed out by Elton (1927) in his discussion of the dispersal of animals, " . . . only a tiny fraction of the original emigrants will ever succeed in establishing itself even temporarily. . . "

For any animal, the limiting factors in different regions may differ. Thompson and Parker (1928) in their studies of the parasites of *Pyrausta nubilalis* concluded that a parasitic species may be limited to different hosts in different regions and that in different regions the parasitic fauna of a host may differ both quantitatively and qualitatively. Observations by Clark and Bradley (1939) indicate that *Chelonus annulipes* can exist as a parasite of *P. nubilalis* only in more or less restricted ecological areas. Establishment in a region containing such areas depends to a large extent on the close spacing of the colonies.

Introduced parasites are usually artificially colonized, that is, "established as individuals," under the most favorable conditions obtainable. Full-fed, mated females, ready to oviposit, are placed in close proximity to a natural host which is in a stage susceptible to attack. It is in "establishing themselves as species" that they encounter the most resistance.

Since parasitic insects usually have a climatic range approximately the same as that of their natural host species, it follows that most introductions meet with little, if any, *direct* resistance from temperature or moisture. Parasitic introductions which apparently have failed in establishment because of desiccation or because of inability to survive winter conditions are probably

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[1]Environmental resistance, as generally conceived, is simply resistance to the *growth* of populations. In the case of established species environmental resistance *regulates* the *densities* of populations (Smith, 1935).

[2]Paper No. 410, University of California Citrus Experiment Station, Riverside, California.

[3]Assistant Entomologist in the Citrus Experiment Station.

exceptional. The resistance from climate, however, may often be *indirect* in causing a lack of synchronization between the attacking stage of the parasite and the susceptible stage of the host (Clausen, 1936).

The habitat responses of the ovipositing female appear to be of fundamental importance in relation to environmental resistance.

Wheeler (1911) has pointed out that the outstanding peculiarity of insect parasitism is the specialization of the *free* adult for the purpose of disseminating the species and of placing the coming generation in contact with the host. This is equally true of phytophagous[4] and of entomophagous species.

The free adults of both groups are similar in their habitat responses. The newly emerged adults of each generation are able to leave the environment of their development and to return under the urge to oviposit. The principal difference in habit exhibited by the adults of the two groups is in oviposition. In some entomophagous species there is little if any difference even in this respect, oviposition occurring directly on host-free plant tissue. On the other hand, oviposition by *Eurytoma parva*, the larvae of which usually attain maturity only by feeding on wheat stems, is restricted to plants in which *Harmolita tritici* has oviposited (Phillips, 1927).

When produced under insectary conditions, the gravid female parasites are confined to the vicinity of the host. For establishment in the field, they must also be confined, for a time at least, to the host habitat. That this is a fact is indicated by the observations of Picard and Rabaud (1914), that in the case of certain parasites the attraction exercised by the plant frequented by the host is of greater importance than the attraction exercised by the host. As Laing (1937) observed, parasites first "find" a certain type of environment and then proceed to locate a medium for the deposition of their eggs.

In order for a parasitic species to become established, it is obvious that the ovipositing female must frequent the type of environment that contains its host. The type of environment frequented by the female seems to be determined by the state of ovarian development. Parker (1918) observed this to be the case with *Chloropisca glabra*. The experiments of Thorpe and

[4]Unlike most phytophagous insects, coccids are disseminated only when very young, by wind and other agencies.

Caudle (1938) with *Pimpla ruficollis* show a correlation between the type of environment frequented by the female and the degree of ovarian development. This is probably a common phenomenon. An interesting example is reported by Clausen and Berry (1932), who found that the adults of the citrus blackfly mate and feed almost exclusively on fresh young leaves, and that the gravid females then descend to the more mature foliage for oviposition.

In general, it is this process of host finding, as pointed out by Salt (1938), that removes by far the largest number of species from the potential host list of a parasite. Because the artificial conditions of the laboratory tend to interfere with the natural processes of host elimination and host finding, the laboratory host list is apt to be larger than the natural host list. It is partly for this reason that biological control workers too often find that the facility with which a parasite is propagated in the insectary is not predictive of its establishment, even in a habitat which contains a host species apparently unprotected and in a condition for parasitization.

It is reasonable to assume that parasites are most readily established in habitats similar to those in which they are indigenous. It has often been observed, however, that insects frequent different food plants in different climatic regions; that in one region a plant species is never infested, whereas in another it is often infested. There is no reason to believe that the habits of entomophagous insects differ in this respect from those of phytophagous species.

It is significant that most introduced species reproduce for at least one generation when the colonizations consist, in part, of mated females in condition to oviposit and are placed in contact with a suitable host. The establishment of such species will not occur, however, if a suitable niche[5] is lacking; that is, if (1) the host habitat is unfrequented by the colonized parasite, or (2) the host is absent in the habitat frequented by the colonized parasite. If a suitable niche is available, establishment will be prevented by conditions which inhibit (1) the deposition of fertilized eggs by the colonized parasites or (2) the development of the progeny of the colonized parasites.

[5]The term "niche," as used in this paper, is in no sense a synonym of "habitat," but is used as by Elton (1927) "to describe the status of an animal in its community, to indicate what it is *doing* . . . ." In other words, "the 'niche' of an animal means its place [rôle] in the biotic environment."

HOST HABITAT UNFREQUENTED BY COLONIZED PARASITE

Colonization of a parasite on a host-infested plant species which is not attractive to the parasite adult is not likely to result in establishment. Such a lack of trap-action may explain, in part, the fact that the black scale, *Saissetia oleae* (Bern.), in some citrus groves in southern California is inadequately controlled by parasites.

Compere[6] informs me that in Asia, Australia, Africa, and South America (Compere, 1939), as well as in California, he has found black scale on different plants in different climates. In Africa, which is considered to be the native habitat of black scale, infestations are rare, although at least two dozen native and introduced plants are known to be hosts. Citrus, however, is not a host of black scale in Africa. This fact is attributed by Compere (1940) to unknown environmental factors and not to parasites.

Under insectary conditions, citrus is unsuitable for the propagation of black scale, since very few scales reach maturity upon this host. Oleanders, on the other hand, are extensively used for this purpose. Nevertheless, in certain sections of California where citrus is periodically infested, oleanders are rarely infested.

It is notable that a South American tree, *Schinus molle* (pepper tree), upon being introduced into southern California, became a suitable food plant for black scale, although Compere informs me that in its native habitat this tree appears to be free of this scale. Severe infestations were general in southern California until the introduction of African parasites, particularly *Metaphycus lounsburyi* (How.). At present, pepper trees are usually free of black scale, even when adjoining citrus trees are infested. This is possibly the result of a difference in the attractiveness of the two habitats to the parasite adults.

A pest is subject to control by parasites if it infests plants frequented by its parasites, but if the habitat of the host has no attraction for the parasite, attempts to establish the parasite are likely to be futile.

HOST ABSENT IN HABITAT FREQUENTED BY COLONIZED PARASITE

The habitat frequented by a parasite may lack hosts because of natural influences or because of artificial treatment. In its native environment, a parasite tends to confine its search to plant or animal habitats which usually contain its host. In a new invironment, such habitats may be free of hosts.

The presence of uninfested plants having greater attractiveness than infested plants may prevent the establishment of the colonized parasite.

If a parasite spends too much time in useless searching, ovarian degeneration may occur, and with it, the loss of the urge to oviposit as well as the loss of the ability to locate hosts. *Comperiella bifasciata* How. is an effective parasite of yellow scale, *Aonidiella citrina* (Coq.), on citrus, but its spread from point of colonization has been slow. This may be partly the effect of searching large areas of leaf surface quite free of hosts.

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[6]Compere, Harold. Associate in the Experiment Station (Entomology).

A resisting factor, the importance of which should be emphasized, is the application of effective insecticides which create host-free areas. If the host-infested area used for colonization is small and is surrounded by extensive host-free areas, liberations of effective parasites may be abortive because of the dispersion and consequent loss of the liberated individuals and their progeny.

The effect of weather or insecticides on the population of a plant pest may be catastrophic, not only upon the pest, but upon its parasites—the effect on the parasite resulting from the destruction of its host. The interruption of host reproduction handicaps its natural enemies (Clausen, 1936). The application of an insecticide, by interrupting host reproduction through destruction of the host species, may result in the elimination of the parasitic species. Consequently, the application of insecticides tends to perpetuate the periodic necessity for their use. As pointed out by Nicholson (1937), "All our experience of controlling pests shows that if a pest is reduced to a low density by artificial means, these artificial means must be maintained indefinitely if the pest is to be maintained at a low density." The lack of food (hosts) may so reduce an effective parasite population that the host population can subsequently reach a high density and cause serious damage before the parasite regains control. Clausen's observations support this proposition, that insects normally held to a low population level by natural enemies may become pests through the use of insecticides. If the host population is reduced to a level lower than that needed to support the parasite, periodic outbreaks of the host inevitably follow.

Clausen (1936) cites an example of the effect of using an insecticide against a pest under control by parasites. In Malaya, the citrus blackfly, *Aleurocanthus woglumi*, is controlled by parasites. Several orange trees, however, were found to be heavily infested, and some of the trees were sprayed periodically with kerosene emulsion. On these trees the infestation repeatedly attained the maximum within a few months. On the other hand, the trees left unsprayed were almost completely free from blackfly three months after the first observation and remained so for at least two years.

Orr (1931) found that the use of oil sprays for the control of the pine tortoise scale, *Toumeyella numismaticum*, inhibited the reproduction of its natural enemies.

In California, complete biological control followed the introduction of *Rodolia cardinalis* and *Cryptochaetum iceryae* against the cottony cushion scale and the introduction of *Coccophagus gurneyi* and *Tetracnemus pretiosus* against the citrophilus mealybug (Smith, 1933). The success of these introductions and the rapidity with which control was attained probably were due in large part to the fact that the hosts could not be controlled by insecticides. If the insecticides now used so extensively and thoroughly in California to control red scale, *Aonidiella aurantii* (Mask.), black scale, and citrus red mite, *Paratetranychus citri* (McG.), were sufficiently lethal to cottony cushion scale, *Icerya purchasi* Mask., and the citrophilus mealybug, *Pseudococcus gahani* Green, it is possible that these two last-named insects would again become chronic pests.

In most cases, the lethal effect of an insecticidal application on the *adults* of an established parasite is probably of minor importance.

Clausen and Berry (1932) attempted to maintain a population of citrus blackfly on several infested trees by poisoning the adult parasites with a sweetened arsenic compound. Nevertheless, "The females apparently were able to effect a considerable oviposition before dying," so that in a few months the blackfly was "at the point of virtual extinction." Catastrophic control through the use of insecticides which are not lethal to the parasite pupa or adult may be superior *in effect* because of the subsequent mopping-up action of the parasites surviving treatment. Clausen (1936) has pointed out the superiority, in this respect, of organic materials as compared with inorganic materials, where repeated applications are made.

Observations during the past eight years on the relation of *Comperiella bifasciata* How. to its host, the yellow scale, have shown that in orchards where insecticidal treatment is withheld long enough to permit the scale to become abundant, the parasite then cleans up the scale within two or three years. Such orchards have remained commercially clean because the parasite permeates the host habitat, and the host is always present in sufficient numbers to support the parasite. The colonization of *C. bifasciata* in orchards periodically treated for yellow scale is useless.

Collins (1934) found that the use of sprays that were effective against the codling moth reduced the parasitism by *Ascogaster carpocapsae* in the order of their effectiveness against the host. On the other hand, repeated applications of arsenical preparations do not seriously affect the increase and spread of the woolly apple aphid parasite, *Aphelinus mali* (Clausen, 1936), since such insecticides are not lethal to the host.

In certain sections of California the necessity for treating citrus orchards in the control of red scale interferes with the natural control of certain citrus pests. This situation probably will exist until an effective parasite of red scale is established, or until an insecticide is developed that is effective against red scale but not injurious to other pests.

At present, periodic treatment for red scale destroys incipient populations of black scale. In areas free from red scale, the control of black scale may be left to the natural enemies, provided an effective species is present. In several orange groves in southern California, black scale is under natural control. These groves are commercially clean most of the time.

Since it is impracticable to produce and liberate enough parasites to obtain immediate establishment throughout a large area, such production must take place in the field. Unfortunately, the density of the host population required for the establishment of an effective parasite population may result in a considerable loss to the grower.

It has been found that the establishment of black-scale parasites is difficult, if not impossible, in orchards where an insecticidal control program is religiously carried out.

Failure in establishment may result, also, from the lack of a necessary alternate host. Howard and Fiske (1911) believed that such was the cause of the failure of *Apanteles fulvipes* to become established as a parasite of the gipsy moth. Clausen and King (1927) state that success

in establishing *Campsomeris annulata*, a parasite of *Popillia japonica*, will depend upon the abundance of alternate hosts.

INHIBITED DEPOSITION OF FERTILIZED EGGS BY COLONIZED PARASITES

Although the black scale is a relatively inert host, the individuals of a population may exhibit a comparatively wide variation in the character of the attributes which bring about a preferential response on the part of the female parasite. Hymenopterous parasites tend to deposit *fertilized* (female) eggs only on preferred individuals of a host species (Flanders, 1939). Factors, such as a cover of dust, small size, or age, that cause the host to become unpreferred decrease the possibility of establishment, since *unfertilized* (male) eggs are deposited on unpreferred hosts.

The two types of cocoons constructed by the codling moth may account for the failure of its parasite, *Calliephialtes* sp., to become established when it was distributed in large numbers throughout California twenty-five years ago. Recent observations at the Citrus Experiment Station indicate that *Calliephialtes* deposits only unfertilized (male) eggs in cocoons made by non-overwintering larvae of the codling moth.

As Salt (1937) has shown in the case of *Trichogramma*, oviposition by one individual may be inhibited by the influence of other individuals of the same species. The first female to attempt oviposition upon a host may, without actually depositing an egg upon it, render it repellent to succeeding parasites. Investigations under way at the Citrus Experiment Station indicate that this is a common phenomenon.

The food requirements of the adult parasites may prevent the establishment of the species. Gardner (1938) reports that the Japanese beetle parasite, *Tiphia vernalis*, rarely becomes established in areas where there are no aphids to produce the honeydew upon which the adults of *Tiphia* feed almost exclusively. Oviposition in such species is probably dependent upon an adequate supply of carbohydrates.

The release of small numbers of parasites in habitats in which predators, such as spiders or ants, are abundant may result in the destruction of the adult parasites before they can oviposit.

INHIBITED DEVELOPMENT OF THE PROGENY OF COLONIZED PARASITES

The suitability of a host for the development of its parasite may be affected by the host plant. Gilmore (1938) has shown that *Protoparce sexta*, the normal host of the braconid *Apanteles congregatus*, when fed on dark-fired tobacco, became unsuitable for the development of the parasite. I have observed that the red-scale parasite, *Habrolepis rouxi* Comp., rarely completes its development in red scale grown on *Cycas revoluta*, although in red scale grown on citrus its development is usually complete. Under field conditions, I have observed that black scale infesting citrus is highly parasitized by *Coccophagus rusti* Comp. when on rapidly growing wood (suckers). This may be the effect of low mortality of the developing parasite.

Since the parasitization of a pest may be determined by the kind of

host plant or by the condition of the host plant, it is possible that black scale growing on citrus under certain field conditions is more or less unsuitable for parasite development.

When imported black-scale parasites are liberated in black-scale infestations of several years standing, they may encounter great competition from species already established. This competition reduces the rate of increase and, if the liberations are small, may eliminate the colony.

In California, the presence of the primary endoparasites *Coccophagus scutellaris* (Dal.) and *Metaphycus lounsburyi* (How.) may prevent the establishment of other primary endoparasites intrinsically inferior. In several instances liberated stocks of parasites apparently have failed in establishment because of a lack of black scale resulting from the work of parasites already present. It is evident that the facility of parasite establishment is affected by the extent to which other species occupy the available niches in its new environment.

"Secondary parasites [hyperparasites] often greatly retard the increase of valuable primary parasites and may seriously interfere with the successful establishment of the latter in a new country" (Muesebeck and Dohanian, 1927). They attack host parasites in many different niches. In California, hyperparasites, such as *Cheiloneurus noxius* Comp., *Eupelmus inyoensis* Gir., *Eusemion californicum* Comp., *Quaylea whittieri* (Gir.), *Tetrastichus blepyri* (Ashm.), *Marietta mexicana* (How.), and *Thysanus* sp., if abundant, may destroy new colonies of primary black-scale parasites. The destructive effect of hyperparasitism, however, as well as that of competing primary parasites, may be largely avoided by colonizing the introduced parasite in "young" infestations of the host.

The principal effect of hyperparasitism is the retardation of the rate of population growth of the primary parasite. When the primary parasite is well established, hyperparasitism may be unimportant. In Africa, for example, the black scale appears to be effectively controlled by parasites, although attacked by a complex of hyperparasites similar to that in California: *Quaylea whittieri* (Gir.) is absent but its niche is occupied by several species of *Baeoanusia*.

SUMMARY

The establishment of parasitic Hymenoptera may be resisted by environmental factors which affect the activity of the ovipositing females or the development of their progeny. A parasitic species may fail to become established because it does not frequent host habitats or because it frequents habitats which lack hosts. The use of insecticides may reduce the host density below that required for the maintenance of the parasite population. Establishment may fail if the deposition of fertilized eggs by colonized adult parasites is inhibited by a change in condition of the host, the presence of predators, or the lack of food; or if the development of the parasite progeny is inhibited by the unsuitability of its normal host or by the competition of other parasites, either primary or secondary.

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THE ROCKY MOUNTAIN "BLACK FLY," SYMPHOROMYIA ATRIPES

(Diptera: Rhagionidae)

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In the 1920's when hiking in the Cascade Mountains in southern British Columbia, I was persistently annoyed by a small, black fly which approached noiselessly and inflicted a painful bite. In that part of the country hikers agreed that at elevations of about three to five thousand feet the discomforts caused by this fly were equalled only by those of mosquitoes, usually with this distinction—when there were mosquitoes there were none of these "black flies"[1] and when these were present there were no mosquitoes. During the summer of 1936, a party of us visited this same range in Washington and were almost completely routed by the same little animal. This time I procured some specimens, and they proved to be the Rhagionid fly *Symphoromyia atripes* Bigot, fig. 1.

The fly apparently attacked only on sunny days and only in the open. On cloudy days or in dense shade where mosquitoes were abundant, this fly was almost completely absent. When it was present, however, this species of *Symphoromyia* inflicted a most painful bite, drawing blood profusely and causing some swelling of the bitten spot. The flies approached noiselessly, often in swarms, but were very easy to kill due to their sluggish movements and persistence when biting. Similar observations have been made on this and related species many times. An interesting compilation of such remarks is given by Aldrich (1915 pp. 114–116).[2] He points out that these flies also bite other mammals. His remarks on the severity of their attack on horses are interesting:

"I found *S. atripes* Bigot very troublesome to horses on the stage road from Ashford, Washington, to Longmires Springs, in

[1]Locally called "black fly" or "deer fly." True deer flies (Tabanidae) are also abundant and annoying in the same region.

[2]Proc. U. S. Nat. Mus., Vol. 49.

the Mount Rainier National Park. This was on August 2, 1905. There were about 100 flies at once hovering about the four-horse team, many biting the horses and a few the passengers. They were most abundant about the horses' heads, and I noticed the blood trickle down from punctures that the fly had left, indicating that the razor-edged mandibles [fig. 9] cut a considerable hole in the skin. I have never seen Tabanidae attack horses so severely."

Most books dealing with noxious insects or medical entomology give no mention of this group of flies. Other books give it passing notice. It is my belief that from the standpoint of human comfort this group is fully as important as Simuliid black flies in many sections of the Rocky Mountains.

Nothing is known about the life history and immature stages of *Symphoromyia atripes*. Presumably these stages are similar to those of European species, which have terrestrial larvae that live in soil, humus or rotten wood. Habits such as these have a peculiar significance—they group the larvae of these blood-sucking flies with some of the lesser known species of punkies, but remove them completely, in an ecological sense, from the aquatic larvae of mosquitoes and blackflies.

Symphoromyia atripes is distributed from California, Utah, and Colorado north to Alaska, is one of the common species of the genus in that region, and appears to be especially abundant in parts of the Cascade Range.

MORPHOLOGY OF THE MOUTH PARTS

The mouth parts are remarkably similar to those of *Tabanus*. The only differences found have been in slight proportions of most of the parts and an absence of several sclerites in the proboscis.

Mandibles (fig. 9).—These have a broad base bearing an elongate, mesal blade which is toothless, flat, smooth and sharp.

Maxillae (figs. 2–4).—These have the cardo fused with the eustipes. The palpus is two-segmented, large and hairy. The eustipes is prolonged into a blade-like galea which bears at the tip a row of very minute teeth. At a point which is probably the boundary between the eustipes and galea there is a thumb-like lobe, probably the parastipes, which bears a long, thread-like filament loosely attached for its entire length to the mesal margin of the galea by weak membrane. This filament is the lacinia, shown slightly teased out in fig. 3.

Labium or proboscis (fig. 6).—The proboscis has no sclerotized plates on its floor. The large sclerite *theca* (th) is apparently the only armature of the mediproboscis. The distiproboscis (dpr) has the labella large and provided with a well developed pseudotracheal system (pt).

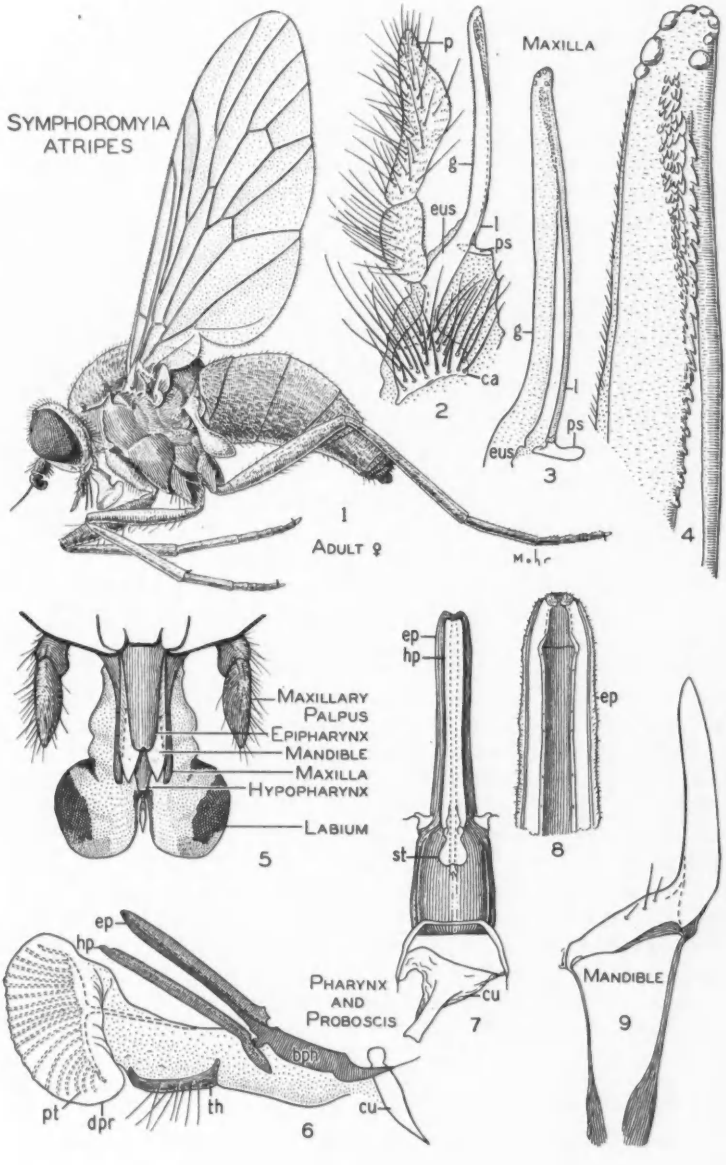
Pharynx (figs. 6–8).—In this structure the similarity to *Tabanus* is striking. The epipharynx is long, fairly wide and pointed at the apex; its underside is provided with a wide concavity which runs its entire length and narrows to a point at the apex. The hypopharynx is the same length but narrower, its extreme base enlarged into the bulbous salituba with which the salivary duct connects. The basipharynx is large and parallel-sided. Blood is undoubtedly sucked up through the channel formed by the appressed hypopharynx and epipharynx as in *Tabanus*. The salivary duct enters the salituba and continues down the entire length of the hypopharynx, emptying almost at the tip.

PARASTIPES AND LACINIA

Previous writers have regarded the small stub labelled *ps* in figs. 2 and 3 as the lacinia. Careful dissection of the maxillary blade of both *Symphoromyia* and *Tabanus* has shown that it is not a simple structure. In the former it is composed of a lateral blade and a mesal filament which are connected by membrane along one side and fused at the extreme apex. In *Tabanus* the blade is composed of a thin ectal and ental blade joined along one margin with membrane and also fused at the extreme apex; the ental blade when teased out is found to be joined to the stub labelled *ps*. This seems good evidence that we have here a true parastipes and lacinia, and it is probable that this interpretation will apply in many groups of Diptera.

ABBREVIATIONS USED IN PLATE

bph—basipharynx.
ca—cardo.
cu—cornua.
dpr—distiproboscis.
ep—epipharynx.
eus—eustipes.
g—galea.
hp—hypopharynx.
l—lacinia.
p—palpus.
ps—parastipes.
pt—pseudotrachea.
st—salituba.
th—theca.


SYMPHOROMYIA ATRIPES
1
ADULT ♀
MAXILLA
p
g
eus
l
ps
ca
2
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MAXILLARY PALPUS
EPIPHARYNX
MANDIBLE
MAXILLA
HYPOPHARYNX
LABIUM
5
ep
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PHARYNX AND PROBOSCIS
cu
7
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MANDIBLE
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bph
pt
dpr
th
6

STUDIES ON THE POISON SYSTEM OF THE HONEYBEE

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Our usual interest in the poison system of the honeybee, *Apis mellifica* Linn. lies generally in the cause and effect of the sting rather than in any possible relationship between this complicated system and the general physiology of the organism to which it belongs. The severe and sometimes fatal after-effects of the sting of the bee is a matter of rather commonplace record. Considerable information is also available on the beneficial effects produced by a controlled application of the venom on certain organic disorders of man. In these investigations no exact chemical analysis of the poison synthesized by the honeybee seems to have been made and even less information is available on the possible relationship of the substance itself to the insect other than its protective role.

Cheshire[1], Snodgrass[2] and others have illustrated and described in some detail the various parts of the poison system of the honeybee, including the cellular structure of the acid and alkaline glands in which the poison is engendered and the apparatus in which it is blended and administered. In none of the works reviewed personally have we found any reference to certain bodies that occur on a fairly large proportion of the acid glands of the honeybee nor have we discovered any mention of certain physical changes which occur naturally or which develop in the queens and workers, under special environmental conditions.

Our attention was first attracted to this study by a search for observable physical factors in queens which might indicate the cause of their premature supersedure. While our investigations are by no means complete we feel justified in publishing a portion of the results in order to call the phenomena to the attention of other investigators engaged in a study of similar problems.

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[1]Cheshire, Frank R. 1886. Bees and Bee-keeping, Scientific and Practical. Vol. I 336 pp.

[2]Snodgrass, R. E. 1925. Anatomy and Physiology of the Honeybee. McGraw-Hill, 327 pp.

THE POISON OF THE BEE STING

The food of the honeybee consists almost entirely of water, carbohydrates, in the form of dextrose, levulose and sucrose secured from nectar, and proteins secured from pollen. The necessary minerals in its diet are undoubtedly secured from nectar, water and pollen. The diet of the queen is made up largely of these materials predigested by the nurse bees. From these materials, poison must be produced by metabolic processes of various organs of the body and particularly by the acid and alkaline glands which empty their fluids into the base of the sting. Beck[3] has assembled comprehensive details concerning the chemical and physical properties of bee venom and the complexity of the substance can be deduced from the following description: "Bee venom is a water-clear liquid with a sharp, bitter taste and aromatic odor, having a distinctly acid reaction. Its specific gravity is 1.1313. It is easily soluble in water and acids, almost insoluble in alcohol. It contains 30 per cent solid matter. The weight of an average drop of venom is about 0.2 to 0.3 mg., that is, about 1-500th part of the bee's body weight. The venom dries quickly in ordinary room temperature. Drying will convert it into a gum-like substance, without any loss of potency. It is very thermostable, withstanding 100 C. temperature for 10 days without losing any of its power. Boiling will make clear venom cloudy, but if boiled in a sealed glass tube even for two hours its appearance will not be affected. Cold, even freezing, does not destroy its effect. It cannot be dialyzed through a membrane, which signifies that it belongs to the colloidal group. By various manipulations the venom gives a sediment rich in albumin. In addition to albumin, bee venom contains inorganic salts, sodium, and calcium, besides hydrochloric acid, phosphoric acid, volatile oils and a very toxic organic base—a nitrogen-free compound—which is the effective part. Flury, in 1920, through hydrolysis of Langor's base (bee venom in an albumin-free state) with hydrochloric acid, found in it the following substances: tryptophan, chlorine, glycerine, phosphoric acid, palmitic acid, fatty acid, (non-crystallizable), a volatile acid, likely butyric, and a non-nitrogenous substance."

Whether this poison is synthesized in the cells of the acid

[3]Beck, Bodog F. (M. D.) 1935. Bee Venom Therapy. D. Appleton-Century Co. N. Y. 238 pp. (A rather extensive bibliography is given in the book.)

and alkaline glands directly from food elements selected by them from the blood stream or from certain waste products of metabolism is unknown at the present time. We also know little of the total amount of poison produced during the lifetime of the honeybee or whether or not it is produced and then eliminated at times other than through the stinging process. Examination of pupae indicates that the poison is present in the poison sac some time before the imago emerges from its cell. This is especially true in the case of queens which have a larger poison system than the workers and generally have a greater supply of the poison, although they seldom have occasion to use it either defensively or offensively. We also know little of the relative potency of bee venom in respect to the age of the honeybee or in relation to its food supply. The sting of the honeybee is known by beekeepers to be "hotter" at certain seasons of the year and while bees are working on various plant sources. In California, the sting of bees is especially potent while they are working on the California buckeye, *Aesculus californicus*, the pollen and nectar of which is deleterious to the adults and to the brood.

THE ACID GLANDS OF THE HONEYBEE

The acid gland of the honeybee is a thin, normally white, bifid, tubular organ attached to the poison sac which empties into the base of the sting. The gland of the worker generally lies in a dorso-lateral position in the right side of the abdominal cavity, generally entwined with the malpighian tubules and lying against the ventriculus. In queens the two branches are usually on either side of the median line. The gland is well supplied with tracheae which tend to hold it in place in the body cavity. It has many twists and turns and is quite elastic thus making it difficult to secure an accurate measurement of its length. Cheshire reported the worker gland to be 1¼ inches in length and that of the queen 1½ inches. Our measurements indicate a much smaller size when measured without any stretching. The average length of 100 Italian worker glands was 14.26 mm. divided into a main stem of 12.8 mm. and two branches, 1.5 and 1.2 mm. in length. The glands of 92 Caucasian workers measured 12.8 mm. for the main stem and 2.2 and 1.8 mm. for the two branches, a total of 15.0 mm. The glands of 32 queens averaged 4.7 mm. for the main stem and 29.5 and 30.4 mm. for the two branches, or a total length of 35.0 mm. The worker glands varied from 7.5 mm. to 28.5 mm. with those of the Caucasians being as variable as the Italians. The length of the glands of the queens varied from 20.0 mm. to 57.0 mm. The glands could have been stretched to approximately twice the measurements given above, and if an allowance were made for the many small curves, the total length would have greatly exceeded the measurements given.

From these measurements, however, it will be seen that the glands of the worker and of the queen differ materially. In the case of the worker there is a rather long main stem and two short branches while in the queen, the main stem is short and the branches are relatively long. In both the worker and queen there will often be found nodes or short branches arising from the main branches as indicated in figures 4, 5 and 6. Instances were observed in both workers and queens where there was no main stem to the gland, the two acid glands emptying into the poison sac at separate points. While the glands usually end in a slightly enlarged oval, as in figure 3, the terminal points are at times more complex, as indicated in figures 4 and 5.

Both glands are composed of a lumen surrounded by cells containing relatively large nuclei, figures 10 and 12. Preparation of the glands with a 4 per cent potassium hydroxide solution did not reveal the ductlets as described by Cheshire. The glands stained readily with fast green and haemalum. Alcohol immediately solidified the poison in the poison sac and stiffened the glands to a point approximating brittleness. The glands became flexible again when placed in acid-alcohol. The poison in the poison sac likewise stained readily but was not easily sectioned.

In 1936, the writer[4] demonstrated that when queens were exposed to cold for various periods of time, they were injured to such an extent that their colonies soon started to supersede them. Further examination of similarly treated queens indicated that the main evidence of injury generally centered in the acid gland which often turned black in various portions. Worker bees were likewise affected to a considerable extent (figure 11). The injury is not always evident until some weeks after exposure although in certain instances the color change was noted within a few hours.

NORMAL AND ABNORMAL GLANDS

The examination of various queens returned from Canada or which were sent in for examination by California beekeepers or those taken from our own colonies because of a failure of the queen to perform normally, revealed, in many instances, only an injured poison gland or an abnormal poison sac. This led us to an examination of normal queens in order to determine how prevalent certain apparent abnormalities existed under average conditions of breeding and colony management. Since the poison systems of the worker and queen are similar structurally, worker bees were likewise examined for the occurrence of certain abnormalities that were found in queens.

[4]Eckart, J. E. 1936. Preparation, Shipment and Installation of Package Bees, Jour. Econ. Ent. 29 (5): 877–885.

In a large percentage of normal queens and workers, the acid gland was white throughout its entire length and the poison sac was transparent and filled with a water-white poison in liquid form. This condition obtained in a majority of all apparently normal queens and worker bees examined. At the same time, the acid glands and poison sacs of some workers and queens were found to have irregularly shaped black or brownish-black spots attached to the outside or imbedded in the cells and a minor proportion had some discoloration of a portion of either the acid gland or the poison in the poison sac. An examination of pupae after the formation of the poison system and of recently emerged queens revealed the presence of similar spots on the acid gland and poison sac but no discoloration of either. These dark spots were insoluble in alcohol, xylene, and cold potassium hydroxide. Figures 1, 2, 7, 8, 9, 10 illustrate the shape and relative sizes of the spots thus observed. The spots were often so small and so few in number as to escape the attention of an observer unless a particular search was made for them with the aid of a dissecting microscope.

An examination of failing queens indicated a larger proportion of abnormal acid glands and poison sacs than in normally vigorous queens. Where a general discoloration occurred in the

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EXPLANATION OF FIGURES 1–12

Fig. 1. Acid gland of worker honeybee containing many dark spots and 3 slightly enlarged areas. A, portion of the poison sac; B and C, enlarged areas. (5 × oc. and 16 mm. obj.)

Fig. 2. Portion of figure 1 indicated by the arrows. A, deposit of brownish-black material. Cells shown in outline only and with other dark bodies scattered through portions of the gland. (5 × oc., 4 mm. obj.)

Fig. 3. Average shape of the apical end of worker or queen acid gland; 4 and 5, occasional shape of apical end of acid gland of queen; 6, illustration of nodes frequently seen on acid gland of both worker and queen. (10 × oc. and 32 mm. obj.)

Fig. 7. Poison sac of a queen with many irregularly shaped darkened areas or spots. (6 × oc., and 32 mm. obj.)

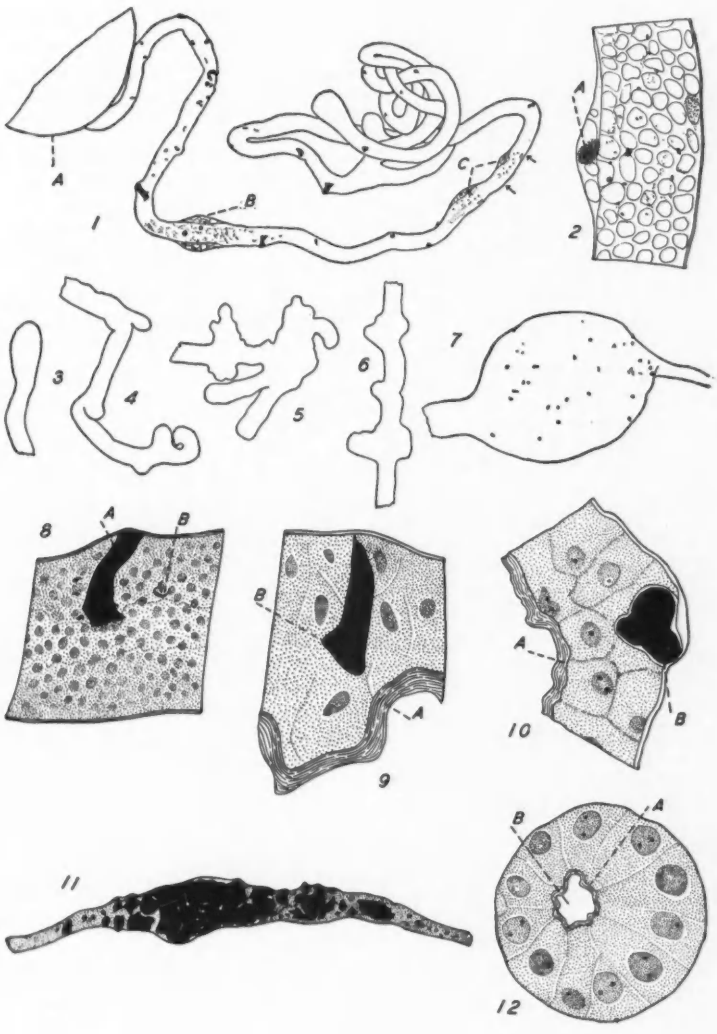
Fig. 8. Portion of whole mount of acid gland of worker under oil immersion showing forms of dark spots, A and B.

Fig. 9. Section from a section of the poison sac of a queen, under oil immersion. A, intima; B, dark spot.

Fig. 10. Portion of a section of an acid gland of a newly emerged queen, the section being near the union of the branches and main stem, illustrating the cellular structure and A, intima; B, darkened portion. (Oil immersion.)

Fig. 11. Portion of a worker acid gland of honeybee that was darkened and hard. (5 × oc., and 16 mm. obj.)

Fig. 12. Section of a branch of the acid gland of a newly emerged queen. (10 × oc. and 4 mm. obj.)



FIGURES 1–12

acid gland, closer examination often revealed the presence of irregularly shaped bodies that at times completely filled the cells and lumen and varied in color from a light brown to black. (fig. 11). Such portions of the acid gland were frequently hard and apparently functionless. In some instances, the cells themselves were enlarged so as to make a distinct swelling at the point of deposit, as illustrated in figure 1–B, C, and figure 2. These darkened portions were frequently, but not always, found in the glands of queens and workers that had been exposed to 34° F. for a period of 5 hours or more, increasing in frequency of occurrence with an increase in the exposure. They were also found occasionally in workers as detailed later. A few specific examples of numerous observations will more clearly illustrate the conditions that have just been described.

EXAMPLES OF INJURY TO QUEEN BEES

1. Dissection of 22 young laying queens from normal nuclei showed 15 individuals or 68 per cent with unspotted glands and 7, or 31 per cent, with glands sparsely spotted. No gland was discolored. Only one of the poison sacs had a few black spots and none contained discolored poison.

2. Of 18 virgin queens confined to nursery cages for 30 days, 10 had the acid gland with a few black spots and 7 poison sacs with similar spots. No gland or poison sac was discolored.

3. In 18 queens between one and three days of age, 13 glands and 7 poison sacs were unspotted and none were discolored.

4. Of 42 worker bees selected at random from colonies, 59 per cent of the acid glands and 95 per cent of the poison sacs were free of spots and only 1 acid gland was slightly discolored.

5. Of 12 normally old but still prolific queens caged from producing colonies, in a study of the effect of caging on their egg production, all poison systems were normal in appearance but one in which the poison sac was filled with an amber colored liquid.

6. When 25 queens that had passed through a season of buckeye poisoning[5] were examined, 11 had the poison sac and acid gland clear, 10 had the irregularly shaped black bodies scattered along the acid gland, 3 had the acid gland and poison sac discolored (amber) and 1 had the acid gland darkened in a small section.

7. An examination of the poison system of 232 queens received from Canada in 1938 gave the following results: those with clear poison sacs, 71 per cent; poison sacs with black spots, 24 per cent; and with discolored poison in the sacs, 4.5 per cent. Only 9 per cent had the acid gland free of spots, 85 per cent of the glands had a varied number of black spots and 5 per cent of the glands had blackened areas. The

[5]Eckert, J. E. 1933. Buckeye poisoning of the honeybee. Jour. Econ. Ent. 26 (1): 181–187.

queens had been caged for 6 to 8 weeks in regular colonies before the close of the honey producing season. The queens were preserved in alcohol on being removed from their colonies.

8. In another lot of 31 experimental queens returned alive from Canada, after having gone through a honey season and six weeks of being caged in their colonies, only 8 had acid glands free of black spots and the balance had a varied number of from a few to many black spots scattered over the acid gland. None of the glands or poison sacs were discolored.

9. Thirty-three out of 37 workers that survived an exposure of 34° F. for 22 hours had portions of their acid glands to turn dark and quite hard. In one specimen a black discoloration was quite noticeable on the ventriculus where the blackened acid gland had been lying.

10. Of 6 queens exposed to 34° F. for 8 hours on June 21, all six produced a large portion of drone brood in worker cells by August 11, when they were dissected. Five had the acid gland discolored by brownish black substances in the cells and in one poison sac the poison was hard although white. The sixth queen had a clear acid gland and poison sac but showed evidence of injury in the ventriculus. The spermathecae of all 6 queens contained active sperms.

11. Fifty-five young worker bees found crawling in front of a nucleus from arsenical poisoning were dissected and in 4, portions of the acid glands were black and hard.

12. Sixty workers were then fed on sodium arsenite and sirup and after they were stricken, but still alive, 7 were found to have the acid gland partially discolored a brownish-black and one gland was darkened throughout its entire length.

13. Forty-nine bees were poisoned by feeding with sugar sirup solution to which had been added 2.5 per cent of a saturated solution of epsom salts. No general effect was noted on the appearance of the acid gland or poison sac although one bee had the acid gland darkened throughout with black deposits.

14. A queen that was being superseded by the bees was dissected and the only abnormal condition was the presence of dark brown material in both branches beyond the main stem of the acid gland.

15. Two queens that had been produced at Davis, California, in May, 1938, and shipped to Mr. Allen Latham, Norwichtown, Connecticut, and returned to us in an attempt to determine what effect the 6,000 mile trip would have on their productivity, were removed from their colonies in August, 1939. They had maintained colonies of average strength, although one of the queens failed to maintain normal brood rearing toward the last. Neither queen was being superseded. The better queen had the acid gland and poison sac covered sparsely with black spots but no definite discoloration. The second queen had only a few black spots on the acid gland but the poison in the poison sac was hard and dark amber in color.

16. A 2-year old queen that was being superseded by her bees had an acid gland densely covered with irregular black spots and a poison sac hard and amber in color.

17. A queen received from a queen breeder with the notation that she had never laid an egg was found to have a collapsed and hardened poison sac that was dark brown in color. Active sperms were present in the spermatheca.

(In no case was the alkaline gland found changed in any particular.)

DISCUSSION

A careful examination of the irregularly shaped bodies that were found attached to or imbedded in the cells of the acid glands and poison sacs of apparently normal as well as abnormal queens and workers indicated no apparent relationship to any definite portion of the cellular structure of either organ. The substances appear to be similar in both workers and queens and apparently were more common in older than in the younger queens examined. The substance varied in color from yellowish brown to black and did not appear to be produced by any bacterial or fungous organisms. They were not artifacts. The data do not indicate any direct relationship between these substances and the general physiology of the organism, since they were present in a large proportion of queens that had produced satisfactory results for one or two years prior to dissection as well as in apparently normal workers. These substances were not found to extend into the lumen of the acid gland or through the intima of the poison sac. They may be melanin pigments.

The condition spoken of herein as discoloration of the acid gland was caused by different appearing substances than the above. The substances appeared to be caused by intracellular chemical changes. The color varied from light brown to black and the size of substance, from small spore-like bodies to material that completely filled the acid gland for a portion of its length or throughout its entire length. Occasionally the discoloration appeared to be centered in the lumen itself. Frequently the gland was hard at the portion so affected. The condition occurred either in the main stem or in the branches. The change in the cell structure is so complete in such portions of the gland that the function of the entire gland must have been affected if not destroyed. In those cases where the gland was black and hard, it apparently was lifeless.

Cheshire[1] stated that in a great majority of the queens he had examined the poison gland was atrophied and the poison sac, although distended, contained only a yellowish substance, almost, if not quite, as solid as new putty. From this he theo-

rized that the poison system of the queen served only during a special phase of her life and his observations suggested that this transpired before impregnation. Wigglesworth[6], in speaking of the relation of certain dermal glands to the general physiology of an insect, conjectures that in some instances, insects have found a biological use for the waste products of metabolism.

The observations of the writer would indicate that the poison system of the honeybee might serve some other function than that of a protective mechanism, especially since an impairment of the acid gland of the queen, in particular, and the poison sac as well, has an obviously deleterious effect on the general physiology of the organism. Such a condition would certainly arise if the poison is elaborated in the glands from substances that would otherwise upset the internal environment of the insect if they could not be removed because of an impairment of the function of the gland or poison sac. The fact that there is no regular elimination of the poison by the bee, as far as we know now, would count against such a theory but would not necessarily nullify it.

When a poison sac becomes hardened, as in some of the cases cited, it undoubtedly ceases to serve as a reservoir for the glands and a certain mechanical impediment would be produced to the normal act of egg-laying. A somewhat similar interference might also result when a portion of the acid gland becomes hardened, but there is apparently a still greater effect on the general physiology of the bee than is caused simply by such mechanical disturbances.

The cause of the development of the darkened areas in the acid gland or of the hardening and discoloration of the poison in the poison sac is a matter for further research to solve. We know that exposure of the adult to certain temperatures for definite intervals will, after a lapse of time, cause the acid glands to become darkened and that this change is accompanied by a marked reduction in productivity and by a general impairment of the physiological condition of the queen. Our evidence, however, does not show conclusively whether the cause of the abnormal physiological condition of the queen is the darkening of the acid gland or an unknown injury to some other system of the organism. The fact remains, however, that in a large number

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[6]Wigglesworth, V. B. Insect Physiology. 1939. Monograph by Methuen. Methuen and Company, Ltd., London. 134 pp.

of the failing queens we have examined for probable causes of failure, the only visible evidence of abnormality was an injured acid gland or poison sac. If the cause of this injury can be found, we may be in a better position to improve the general productivity of our queen honeybees and possibly prevent an abnormal amount of supersedure.

THE MIND OF THE BEES, by JULIEN FRANCON. *Translated by* H. ELTRINGHAM, F.R.S. Pages xi and 146, illustrated by diagrams, 5¼ x 8 inches. 1939. Published by METHUEN & Co., LTD., 36 Essex St., London, W. C. 2. Price 6 shillings net.

This work was first published in France under the title "L'Esprit des Abeilles." The experiments it describes are along the lines of other recent investigations of the abilities and habits of bees. The volume is one of the very interesting books we have read recently. It gives logical explanations, as demonstrated by simple experiments, of what appear at first sight to be remarkable mental ability on the part of the bee. To quote from the translator's preface:

"M. Julien Françon has carried out a series of ingenious experiments designed to answer the question, 'Can bees communicate with each other?' Using sugar as bait, he finds that a bee having once discovered it, can record in her 'memory' both its position in space and the means of access thereto. But what is still more remarkable, he shows that, provided the distance from the hive and the richness of the booty makes it economically 'worth while,' assistant bees will come from the hive to share in the plunder, and that these reinforcements do not necessarily *follow* the original pioneer, but frequently arrive at the scene of operations quite independently."

Apparently bees have the ability to communicate to other workers, and in some detail, the exact location of food and exactly how to avoid obstructions placed to confuse them; also instructions involving color differences. For some of these abilities M. Françon has been able to show their presence but not always has he or any one else been able to give a convincing explanation. His use of red and white as "colors" used experimentally, overlooks the recent work on the spectrum visible to a bee which includes the ultra-violet.

The translator, Eltringham, the noted English authority on the biology of insects, has given us a very simple and easily read translation of a volume which in the first place was written without technical terms. It is a thoroughly scientific volume written in the language of the lay reader. We recommend it to all entomologists as one of the better and simpler analyses of insect behavior.

The chapter headings are often too vague, perhaps a fault of the French original. (However, we have frequently noticed that American editors are more careful to insist on clear and brief headings and titles than are various Continental and even English authors.) Some self-explanatory headings follow:

I. The Methodical Organization of the Work of the Bees.
Chapter 4, The collaborators; 5, The estimate of the produce; * * * 8, The two pitches, or the methodical organization of the forces.

II. Memory, Sense of Orientation, and Survey.
Chapter 9, Memory and sense of orientation; * * * 11, The return to the nest; 12, The survey; 13, A point in space; 14, The absolute necessity of the survey.

III. Bees and Colours.
Chapter 15, Bees and colours.

IV. Intercommunication Between the Bees.
Chapter 16, The principle of the experiments; 17, Simple experiments; 18, Composite experiments; 19, Bees communicate with each Other.

—C. H. K.

A REVISION OF THE NORTH AMERICAN NECYDALINI

(Coleoptera, Cerambycidae)

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The tribe Necydalini comprises those longicorn genera which have very short elytra exposing the abdomen and flat, unfolded wings with three veins in the post-cubital region. The group has been accorded various systematic positions within the family Cerambycidae, the most frequent of which have been either in the Lepturine or Molorchine series. LeConte (1850, 1863) advocated the former arrangement, recent workers have mostly followed the latter. Actually, although the resemblance between the Necydalini and the Molorchini is striking, it is highly superficial. The characters of the larvae, the venation of the wings, and the structure of the adult mouth parts all suggest a relationship to the Lepturinae (and Aseminae) and the tribe is here considered as belonging to that subfamily.

Distribution.—The tribe Necydalini reaches its greatest development in the southern hemisphere, particularly in South America. In the Holarctic Region it is represented by two genera *Necydalis* and *Ulochaetes*. The former genus occurs in both the Old and the New World, the latter confined to western North America.

Habits.—The larvae of *Necydalis* are borers in the heartwood of dying or recently killed trees. One of the North American species breeds in conifers, the remainder in broad-leaved trees. *Ulochaetes* bores in the base and roots of various coniferous trees. It has been reported that the adults of both genera are flower visitors, but the writer has never observed this habit. One of the most interesting features of the adult beetles is their mimetic form and behavior. *Necydalis* so closely simulates an ichneumonid wasp in body form and manner of flight that it is commonly overlooked by the Coleopterist. *Ulochaetes* is equally deluding with its hairy body, robust form, and buzzing, bumblebee-like flight. In both genera the deception is heightened by a "stinging" motion of the abdomen when captured.

Subfamily **Lepturinae** Latreille

Latreille, 1804, Hist. nat. Crust. Ins., 11: 305, *Lepturetae.*
Leach, 1815, Edinburg Encycl., p. 9, *Lepturida.*
Samouelle, 1819, Entom. Usef. Compend., p. 210, *Lepturidae.*
Latreille, 1829, in: Cuvier, Regne Animal, 5: 128, *Lepturetae.*
Stevens, 1831, Ill. Brit. Ent., Mand. 4: 253, *Lepturidae.*
Serville, 1835, Ann. Soc. Ent. France, 4: 197, *Lepturetae.*
LeConte, 1850, Jour. Acad. Nat. Sci. Phila., (2) 1: 313, *Lepturidae.*
C. G. Thomson, 1859, Skand. Coleopt., 1: 150, *Lepturetae.*
J. Thomson, 1860, Class. Ceramb., 143, *Lepturitae.*
J. Thomson, 1864, Systema Ceramb., 140, *Lepturitae.*
C. G. Thomson, 1866, Skand. Coleopt., 8: 45, *Lepturetae.*
LeConte, 1873, Smithson. Misc. Coll., XI, 265: 292, *Lepturoides.*
LeConte and Horn, 1883, Smithson. Misc. Coll., XXVII, 507: 277, *Lepturoides.*
Gahan, 1906, Fauna Brit. India, Coleopt., 1: 2, 68.
Boppe, 1922, Genera. Ins., 178: 11.
Portevin, 1927, Encycl. Ent., 2 (suppl.): 7.

Head oblique, rarely subvertical, gradually or suddenly narrowed behind the eyes; antennae inserted before or between the eyes at a distance from base of mandibles, moderately long, second segment short, transverse; eyes oval, usually entire; mandibles flat, acute, usually with a molar tooth and dense pubescent fringe; maxillae bilobed; palpi with last segment truncate at apex; ligula emarginate, frequently bilobed, membranous or coriaceous; mentum flat, usually trapezoidal; gula produced between base of maxillae as a distinct mentigerous process. Pronotum without a lateral margin; anterior coxae prominent, conical, cavities angulated externally, usually open posteriorly; mesonotum with a stridulating plate usually divided by a median vittae; intermediate coxal cavities open to epinera; metepisterna broad, usually narrowed posteriorly. Legs usually slender; anterior tibiae without a mesial sinus; tarsi pseudotetramerous, padded beneath (pads sometimes lacking on first segment), paronychium absent. Elytra usually narrowed posteriorly, rarely abbreviated, apices variable; posterior wings with or without a closed cell in the anal sector, radial cell closed, veins $2A_1$ and $2A_2$ present, 1A connected with $2A_{1+2}$.

The large subfamily Lepturinae is dominant in the northern hemisphere. The larvae are mostly decaying-wood feeders, the adults usually frequent flowers. The wing venation is very primitive, connecting the Prioninae (through *Philus*) with the *Aseminae* (through *Atimia*). The larvae are more primitive than those of any other group of longicorns, and may be readily recognized by the separate halves of the epicranium. The adults exhibit a close relationship with the Aseminae, but differ in the well developed mentigerous process of the gula.

KEY TO TRIBES OF LEPTURINAE

1. Mandibles short, broad, without an internal pubescent fringe....**Desmocerini**
   Mandibles slender, acute, with a pubescent fringe along inner margin.....2
2. Elytra entire; wings folded at apex; stridulatory plate of mesonotum divided; mentum trapezoidal.....**Lepturini**
   Elytra abbreviated, scarcely extending over base of abdomen; wings not folded; stridulatory plate of mesonotum entire; mentum transverse, **Necydalini**

Tribe **Necydalini** Thomson

C. G. Thomson, 1859, Skand. Coleop., 1: 150, *Necydalina*.
J. Thomson, 1860, Class. Ceramb., p. 169, *Necydalitae*.
Mulsant, 1862, Coleopt. France, Longic., ed. 2, p. 232, *Necydalates*.
J. Thomson, 1864, Systema Ceramb., p. 147, *Necydalitae*.
Fairmaire, 1864, Gen. Coleopt. Eur., 4: 232, *Necydalites*.
C. G. Thomson, 1866, Skand. Coleopt., 8: 47, *Necydalina*.
Lacordaire, 1869, Genera Coleopt., 8: 469, *Necydalides*.
LeConte, 1873, Smithson. Misc. Coll., XI, 265: 325.
LeConte and Horn, 1883, Smithson. Misc. Coll., XXVII, 507: 310.
Leng, 1890, Entom. Amer., 6: 11.
Blatchley, 1910, Coleopt. Indiana, p. 1044.
Reitter, 1912, Fauna Germ., Käfer, 4: 24, *Necydaliina*.
Planet, 1924, Encycl. Ent., 2: 120, *Necydalaires*.
Portevin, 1927, Encycl. Ent., 2 (suppl.): 19.
Scheerpeltz, 1930, Tierw. Mitteleur., 5 (2): 208.
Matushita, 1933, Jour. Fac. Agr., Hokkaido Imp. Univ., 34: 221.

Head constricted behind the eyes; frons large, vertical; antennae inserted high on frons; eyes finely facetted, deeply emarginate; mandibles small, robust, acute, densely fringed along inner margin; mentum short, transverse; ligula membranous, bilobed; palpi short. Pronotum with sides convex or tuberculate, constricted anteriorly and posteriorly; mesonotum with a large, undivided, stridulatory plate; prosternum short, intercoxal process narrow; anterior coxae large, conical, nearly contiguous, cavities open to epimera; metepisterna broad, attenuated posteriorly. Elytra short, scarcely longer than thorax, exposing abdomen, apices dehiscent; wings lying flat on abdomen, not folded at apex, without an anal cell. Legs slender; tibial spurs short; first segment of posterior tarsi without a pubescent sole. Abdomen with tergites corneous; sternites subequal in length, fifth sternite broadly emarginate in male.

The tribe Necydalini may be readily distinguished from the other groups of Lepturinae by the abbreviated elytra, wings which do not fold at the apex, undivided stridulatory plate, and transverse mentum. The two North American genera differ as follows:

KEY TO GENERA OF THE NECYDALINI

Body slender, pronotum sparsely hairy; antennae with fifth segment shorter than third and fourth segments together; palpi with ultimate segment expanded, campanuliform ..... **Necydalis**

Body robust, pronotum very hairy; antennae with fifth segment as long as third and fourth segments together; palpi with ultimate segment oval (p. 279) .... **Ulochaetes**

Genus **Necydalis** Linnaeus

Necydalis Linnaeus, 1758, Syst. Nat., ed. X, p. 421; Serville, 1833, Ann. Soc. Ent. France, 2: 543; LeConte, Jour. Acad. Nat. Sci. Phila., (2) 1: 317; C. G. Thomson, 1859, Skand. Coleopt., 1: 150; J. Thomson, 1860, Class. Ceramb., p. 146; J. Thomson, 1864, Syst. Ceramb., p. 411; C. G. Thomson, 1866, Skand. Coleopt., 8: 47; Lacordaire, 1869, Genera Coleopt., 8: 447; LeConte, 1873, Smithson. Misc. Coll., XI, 265: 325; LeConte and Horn, 1883, Smithson. Misc. Coll., XXVII, 507: 310; Leng, 1890, Entom. Amer., 6: 12; Blatchley, 1910, Coleopt. Indiana, p. 1044; Reitter, 1912, Fauna Germ., Käfer, 4: 24; Planet, 1924, Encycl. Ent., 2: 121; Portevin, 1927, Encycl. Ent., 2 (suppl.): 20.

Form elongate, slender, subcylindrical; integument sparsely hairy. Head broad; antennal tubercles prominent; antennae filiform in the male, shorter than the body in both sexes, eleven segmented, segments three and four together longer than fifth segment, outer segments slender in male with eleventh segment longer than third, expanded in female with eleventh segment shorter than third; palpi with ultimate segment campanuliform. Pronotum feebly to strongly dilated at sides, usually longer than broad. Elytra not covering basal abdominal tergite, together rarely longer than broad, apices dehiscing, usually reflexed. Legs elongate, especially posterior pair; posterior tibiae usually more or less sinuate. Abdomen broad at base, gradually narrowed apically in female, thickened apically in male.

Genotype: *Necydalis major* Linnaeus.

This genus is represented in North America by six species which may be separated as follows:

KEY TO THE NORTH AMERICAN SPECIES OF NECYDALIS

1. Elytra with at most a feeble, transverse subapical impression, apices not reflexed....2
   Elytra with a deep, transverse subapical impression, apices reflexed....3
2. Pronotum dilated, sides strongly tuberculate, as broad as head, at least as wide as long; antennae robust, fourth segment distinctly shorter than third; body robust; integument shining. 20–22 mm. California (p. 272), **barbarae**
   Pronotum subcylindrical, sides feebly tuberculate, narrower than head, distinctly longer than broad; antennae slender, fourth segment subequal in length to third; body slender; integument dullish. 12–21 mm. Eastern North America (p. 273)....**mellita**
3. Pronotum with a distinct longitudinal sulcus; antennal segments five to eleven dilated, much wider than segments three and four....4
   Pronotum without a longitudinal sulcus; antennal segments three to eleven of more or less uniform width....5
4. Posterior tarsi slender, first segment distinctly narrower than apex of tibia; elytral apices with inner angle obtuse; antennal scape globular, outer segments black; 13–23 mm. Pacific Coast from British Columbia to southern California, Arizona, and northern Mexico (p. 274)....**cavipennis**
   Posterior tarsi robust, first segment nearly as wide as apex of tibia; elytral apices with inner angle acute; antennal scape subconical, outer segments red. 15–20 mm. California (p. 275)....**acutipennis**
5. First segment of posterior tarsi slender, at least one and one-half times as long as remaining segments together; antennal tubercles acute above; fourth segment of antennae distinctly longer than scape; elytral apices dehiscing gradually from basal one-third. 15–20 mm. Pacific Coast from British Columbia to northern California (p. 276)....**laevicollis**
   First segment of posterior tarsi robust, about as long as following segments together; antennal tubercles obtuse above; fourth segment of antennae subequal in length to scape; elytral apices dehiscing gradually from apical one-fourth. 13–20 mm. Rocky Mountains and Pacific Coast from British Columbia to southern California (p. 278)....**diversicollis**

Necydalis barbarae Rivers

Necydalis barbarae Rivers, 1890, Entom. Amer., 6: 112; Van Dyke, 1923, Bull. Brooklyn Ent. Soc., 18: 52.

Form robust; color rufous or dark brownish; integument shining. *Head* shining, vertex coarsely punctured; pubescence short, erect,

sparse, fine, golden; antennal tubercles, viewed from front, subacute at apices; antennae robust, longer than body in male, attaining apices of elytra in female, fourth segment shorter than third or fifth, segments three to five expanded at apex in female, cylindrical in male. *Pronotum* as broad as long, dilated at sides with a large, obtuse tubercle, greatest breadth wider than head, disk shining, sparsely, irregularly, moderately coarsely punctured, anterior and basal constrictions finely, moderately closely punctured; metasternum and metepisterna finely, closely punctured, moderately densely clothed with fine, depressed, golden pubescence. *Elytra* nearly plane, without a transverse, subapical impression, together longer than broad; surface coarsely, subcontiguously punctured along basal lateral margin, more finely, sparsely, apically on disk; apices not reflexed, dehiscing suddenly at apical three-fifths, inner apical angle obtusely rounded. *Legs* long, moderately slender; posterior tibiae distinctly curved; posterior tarsi moderately slender, first segment feebly arcuate, twice as long as following two segments together, but little longer than following three segments together. *Abdomen* with sternites finely, closely punctured. Length: 20–22 mm.

Holotype: ♂, No. 299, California Acad. Sci., Ent.; allotype: ♀, No. 300, C. A. S.

Type locality: Santa Barbara, California.

Distribution: coastal central California from Santa Barbara County north to Santa Clara County.

Host: *Quercus agrifolia.*

This species may be easily known by its large size, robust form, heavy antennae, and strongly dilated pronotum. It is apparently rare and only a half dozen specimens have been seen by the writer.

Necydalis mellita (Say)

Molorchus mellitus Say, 1835, Bost. Jour., 1: 194; Harris, 1837, Trans. Hartford Nat. Hist. Soc., 1: 89; LeConte, 1859, Compl. Writings T. Say, 2: 626.

Necydalis mellitus, Haldeman, 1847, Trans. Am. Philos. Soc., (2) 10: 44; Haldeman, 1847, Proc. Am. Philos. Soc., 4: 372 (syn.); LeConte, 1850, Jour. Acad. Nat. Sci. Phila., (2) 1: 317; Leng, 1890, Entom. Amer., 6: 12; Wickham, 1897, Can. Ent., 29: 169; Blatchley, 1910, Coleopt. Indiana, p. 1044; Craighead, 1923, Bull. Can. Dept. Agr. (n. s.), 27: 84 (larva); Van Dyke, 1923, Bull. Brooklyn Ent. Soc., 18: 52.

Necydalis americanus Haldeman, 1847, Trans. Am. Philos. Soc., (2) 10: 44.

Form slender; color piceous, elytra, legs, and abdomen usually wholly or partially rufo-testaceous; integument dullish. *Head* feebly shining; vertex moderately coarsely, closely punctured; pubescence fine, short, erect, sparse, brownish; antennae about as long as body in male, about two-thirds as long as body in female, thicker in female but segments not expanded, scape and apical segments usually reddish, segments three to five subequal in length. *Pronotum* longer than broad, narrower than head, subcylindrical, sides feebly tuberculate, apical constriction broad, deeply impressed on dorsal surface, disk very convex, feebly shining, finely, irregularly, but moderately closely punctate

except for smooth, median, longitudinal sulcus; metasternum and metepisternum opaque, finely closely punctured, obscurely clothed with very fine, short, pale pubescence. *Elytra* nearly plane, with at most a feeble, transverse subapical impression, together about as long as broad, finely, closely punctured, with coarser punctures superimposed, especially on disk; apices not reflexed, dehiscing gradually from basal one-third, inner apical angle rounded. *Legs* elongate, slender; posterior tibiae sinuate; posterior tarsi slender, first segment arcuate, two and one-half times as long as following two together, distinctly longer than following three together. *Abdomen* feebly shining, finely punctured, sternites less regularly punctured than tergites. Length: 12–21 mm.

Type locality: Indiana.

Distribution: Southeastern Canada and northeastern United States south to Virginia and west to Missouri and Iowa. Records: New York: Buffalo, Lancaster, Long Island; Pennsylvania; Maryland: Oakland[1], College Park[1]; Virginia; Indiana: Putnam County, Posey County, Evansville[1]; Michigan: Grand Rapids;[1] Illinois: Brownfield; Missouri: Cadet[1]; Iowa: Sioux City[1], Mt. Pleasant[1].

Hosts: *Quercus, Castanea.*

N. mellita is more slender than the preceding and differs in the narrower pronotum, shorter, more slender antennae with the third to fifth segments subequal in length, elytra which gradually dehisce from before the middle, and the more elongate first segment of the posterior tarsi.

According to Craighead (1923 : 84) this species bores in the solid dead heartwood of oak and chestnut. The larvae are close to those of *N. cavipennis* Lec.

Necydalis cavipennis LeConte

Necydalis cavipennis LeConte, 1873, Smithson. Misc. Coll., XI, 264: 204; Leng, 1890, Entom. Amer., 6: 12; Craighead, 1923, Bull. Can. Dept. Agr. (n. s.), 27: 84 (larva); Van Dyke, 1923, Bull. Brooklyn Ent. Soc., 18: 53; Hardy, 1926, Rep. Prov. Mus. B. C., 1925: 30; Hardy and Preece, 1927, Pan-Pac. Ent., 4: 64 (habits).

Form moderately robust; color reddish brown to black; integument dull; pubescence dense, golden. *Head* dull, closely punctured; frons clothed with fine, erect, golden pubescence; antennal tubercles, viewed from front, obtuse at apices; antennae moderately robust, wholly or with at least apical segments black, much shorter than body in both sexes, scape very stout, globular, fourth segment distinctly shorter than third or fifth, segments five to eleven dilated, wider than segments three and four. *Pronotum* about as long as broad in female, longer than broad in male, apical constriction broad, deep, disk with a median longitudinal sulcus, anterior and basal constrictions densely clothed with prostrate

[1]Records furnished by W. S. Fisher from collection of U. S. National Museum.

golden pubescence; scutellum a little longer than broad, densely pubescent; metepisterna coarsely, closely punctured dorsally, posterior and lower margins finely, closely punctured and densely pubescent; metasternum finely, closely punctured, densely pubescent. *Elytra* dull, a little longer than basal width, dehiscing suddenly from just behind middle, with a distinct transverse subapical impression, punctation moderately fine, close, with coarser punctures in humeral region; apices reflexed, inner angle obtuse. *Legs* elongate, posterior tibiae slightly curved; posterior tarsi moderately slender, first segment less than one-half as wide as apex of tibia, a little longer than remaining segments together. *Abdomen* with sternites dullish, finely, closely punctured, densely pubescent. Length: 13–23 mm.

Type locality: San Francisco, California.

Distribution: British Columbia, Washington, Oregon, California, Arizona, and northern Mexico.

Hosts: *Quercus, Eucalyptus, Alnus, Heteromeles.*

This species is rather variable in color. The female is usually brown and the male tends to be black with bicolored elytra. However, a female at hand from Santa Cruz, California, has the discal pronotal callosities, legs, and basal antennal segments rufous, and a male from Los Angeles has the entire pronotum, elytra, legs, and antennal scape rufous. The Mexican record is based on an example in the collection of Dr. E. C. Van Dyke, labeled Juan Manuel, El Salto Diego, Mexico, elevation 9300 feet, June 3–8, 1937, M. A. Embury, collector.

N. cavipennis is the commonest of the North American species. It breeds in a variety of deciduous trees but is most common in various species of oak. The larvae are heartwood borers and are usually found in stumps or the base of dead standing tree. Observations by Hardy and Preece (1927 : 64) suggest that the species requires two years to complete its life cycle.

Necydalis acutipennis Van Dyke

Necydalis acutipennis Van Dyke, 1923, Bull. Brooklyn Ent. Soc., 18: 51.

Form slender; color black, elytra, legs, and apical segments of antennae rufous; integument shining. *Head* polished; vertex moderately coarsely, closely punctured; pubescence of frons erect, fine, brownish; antennal tubercles, viewed from front, obtuse at apices; antennae moderately robust, much shorter than body in both sexes, scape stout, subconical, fourth segment distinctly shorter than third or fifth, segments five to eleven dilated, wider than segments three and four. *Pronotum* a little longer than broad, apical constriction wide, deep, disk with a median longitudinal sulcus, calluses on each side of sulcus shining, sparsely punctured, anterior and basal constrictions moderately finely, closely punctate, pubescence fine, erect, golden, but

not dense; scutellum a little longer than broad, clothed with golden pubescence; metepisterna coarsely, closely punctured; metasternum a little less coarsely, less closely punctured, clothed with fine, golden pubescence. *Elytra* shining, a little longer than basal width, dehiscing suddenly from middle, with a distinct transverse subapical impression; punctation moderately coarse, close in basal and sutural regions; apices reflexed, inner angle acute. *Legs* elongate; posterior tibiae slightly curved; posterior tarsi robust, first segment nearly as wide as apex of tibia, but little longer than remaining segments together. *Abdomen* with sternites finely, closely punctured. Length: 15–20 mm.

Type locality: Castle Crags, Shasta County, California.

Distribution: California: Shasta County to Tulare County.

Host: unknown.

N. acutipennis is related to *N. cavipennis*, but is more slender and more shining with sparser golden pubescence and the outer antennal segments reddish rather than black. Structurally the two species differ markedly in the form of the tarsi (first segment robust in *acutipennis*), shape of the antennal scape (globular in *cavipennis*, subconical in *acutipennis*,) and the form of the inner angle of the elytral apices. Six specimens, including the type, have been seen by the writer.

Necydalis laevicollis LeConte

Necydalis laevicollis LeConte, 1869, Ann. Mag. Nat. Hist., (4) 4: 383; Leng, 1890, Entom. Amer., 6: 12; Craighead, 1923, Bull. Can. Dept. Agr. (n. s.), 27: 84.

Form very slender; color rufous to black, mandibles piceous, posterior tarsi testaceous. *Head* strongly constricted behind the eyes; genae prominent; surface shining, finely, shallowly, closely but irregularly punctured; pubescence short, erect, sparse, fine, golden; antennal tubercles viewed from front, acute at apices; antennae nearly as long as the body in the male, three-fourths as long as body in female, scape stout, not quite twice as long as broad, remaining segments slender, third segment one and one-half times as long as scape, fourth segment one and one-fourth times as long as scape, fifth segment a little longer than third, remaining segments subequal in length in the male, segments eight to eleven abbreviated in the female. *Pronotum* barely longer than broad, without a longitudinal sulcus, sides feebly tuberculate; surface sparsely clothed with short, fine, erect, golden pubescence, finely, closely punctured except disk, which is polished, nearly impunctate; metasternum finely, closely punctured, finely, sparsely pubescent; metepisterna more coarsely punctured than metasternum. *Elytra* transversely impressed before apex, together as broad as long; surface dull, finely rugose with scattered larger punctures; apices reflexed, widely separated, dehiscing gradually from basal one-third, inner angles obtuse. *Legs* long and slender; posterior tibiae feebly curbed; posterior tarsi with first segment long, very slender, one and one-half times as long as remaining segments together. *Abdomen* with sternites finely, closely punctured, sparsely clothed with fine, short, suberect hairs.

Type: No. 3956, Mus. Comp. Zoöl., Harvard University.

Type locality: "Vancouver's Island."

Distribution: Pacific Coast of North America from British Columbia to northern California. Records: British Columbia: Vancouver, Wellington; Washington: Hoquiam[2], Green River Gorge[2], Bellevue[2], Des Moines[2]; Oregon: Joseph[2]; California: Humboldt County (Orick, Crescent City), Plumas County (Meadow Valley), El Dorado County, (Fallen Leaf Lake), Placer County (Lake Tahoe); Nevada.

Hosts: *Picea, Abies, Pseudotsuga.*

This species appears to be rare in collections and is usually confused with the following. It may be easily distinguished, however, by the gradually dehiscing elytra and structure and proportion of the segments of the antennae and posterior tarsi. Two subspecies are recognizable.

Necydalis laevicollis laevicollis LeConte

This subspecies is characterized by rufous coloration, with only the eyes and mandibles dark. It occurs along the Pacific Coast from British Columbia to Plumas County, California. In the southern part of its territory it appears to be confined to the inland mountain ranges (Cascade and Sierra Nevada Mountains).

Necydalis laevicollis seminiger Linsley, *new subspecies*

Similar structurally to the typical subspecies but black, usually with the elytra brownish and the femora rufous. This race seems to be limited in its range and has thus far been found only along the coast in southern Oregon and northern California.

Material studied is as follows:

(Holotype male, No. 4920, Calif. Acad. Sci. Ent., from Crescent City, California, July 25, 1922; allotype female, No. 4921, from Orick, Humboldt County, California, July 3, 1931; paratypes, one male from the mountains near Orick, July 29, 1935, and one female, Humboldt County, California, July, 1901. All four specimens were collected by Dr. E. C. Van Dyke. Other specimens have been seen from Silver Creek Falls, Marion County, Oregon, July 21, 1938, collected by George Fergison.)

This is the only North American species of *Necydalis* known to attack coniferous trees. It is a heartwood borer. Craighead (1923 : 84) records larvae in the heartwood of living *Picea engelmanni* which they had entered through an old blaze.

[2]Records furnished by W. S. Fisher from collection of U. S. National Museum.

Necydalis diversicollis Schaeffer

Necydalis diversicollis Schaeffer, 1932, Bull. Brooklyn Ent. Soc., 27: 152.

Necydalis laevicollis, Van Dyke, 1923, Bull. Brooklyn Ent. Soc., 18: 52; Hardy and Preece, 1926, Pan-Pac. Ent., 3: 37 (habits); Hardy, 1926, Rep. Prov. Mus. B. C., 1925: 30, Pl. 5, f. 32.

Form only moderately slender; color reddish to black, eyes black. *Head* only moderately constricted behind the eyes; genae scarcely prominent; surface shining, finely, closely, irregularly punctured; pubescence fine, short, erect, pale yellowish; antennal tubercles, viewed from front, obtuse at apices; antennae moderately slender, about three-fourths as long as body in male, a little more than one-half as long as body in female, scape robust, not quite twice as long as broad, third segment about one and one-third times as long as scape, fourth segment subequal in length to scape, fifth segment as long as third, remaining segments subequal in length in male, segments eight to eleven abbreviated in female. Pronotum broader than long, without a longitudinal sulcus, sides scarcely tuberculate; surface sparsely clothed with fine, short, erect and suberect, golden pubescence, denser in apical and basal constrictions; metasternum and metepisterna finely punctured and pubescent. *Elytra* transversely impressed before apex, together not quite as broad as long; surface finely, closely punctured with coarser punctures laterally; apices reflexed, moderately separated, dehiscing suddenly from apical one-fourth, inner apical angle obtuse. *Legs* moderately slender; posterior tibiae feebly arcuate; posterior tarsi with first segment stout, subequal in length to following segments together. *Abdomen* with sternites finely punctured, finely, sparsely clothed with short, suberect, golden pubescence. Length: 13–20 mm.

Type locality: Logan, Utah.

Distribution: Utah: Logan, Vivian Park; Colorado: Mesa Verde National Park; Montana: Missoula[3]; British Columbia: Victoria, Sidney, Goldstream, Okanagan Falls[3], Creston, Duncan, Vancouver Island; Washington: White Rock Springs; Oregon; California: south to San Luis Obispo County (coastal) and Fresno County (inland).

Hosts: *Quercus, Alnus, Rhamnus*[3], *Salix, Eucalyptus.*

This species has long been confused with *N. laevicollis* LeConte but may be readily distinguished by the form of the elytra which dehisce from the apical one-fourth only, the obtuse antennal tubercles, robust first segment of the posterior tarsi, and the short fourth segment of the antennae. The two species also differ in habits, *laevicollis* feeding on conifers, *diversicollis* on broad-leaved trees.

Necydalis diversicollis diversicollis Schaeffer

This subspecies is entirely red (except the eyes) with opaque elytra, the vertex deeply impressed, the elytra less broadly dehiscent, and

[3]Records furnished by W. S. Fisher.

the head feebly constricted posteriorly. The series at hand includes specimens from the Rocky Mountains, British Columbia, and the Sierra Nevada Mountains of California.

Necydalis diversicollis californica Linsley, *new subspecies*

Differing from the preceding by having shining elytra, the vertex less deeply impressed, the head more strongly constricted posteriorly, the elytra a little more broadly dehiscent, the head and thorax more densely pilose, and the male wholly or partly (at least the head and thorax) black.

The material of *californica* is as follows: Holotype male, No. 4922, Calif. Acad. Sci., Ent., from Mt. Diablo, California, May 6, 1937 (Linsley), allotype female, No. 4923, from Oakland, California, May 6, 1927 (Linsley), and five paratypes as follows: one male, Leona Heights, Alameda County, California, July 4, 1916 (Van Duzee), one female, Mill Valley, Marin County, California, July 25, 1935 (Van Duzee), one female, Berkeley, California, August 1933 (Van Dyke), one female, Cazadero, California (Van Dyke), and one male, Oakland, California, May 6, 1927 (Linsley).

N. diversicollis is a heartwood feeder in various deciduous trees. The larvae bore primarily with the grain and are most frequently found in the basal portion of stumps or dead standing trees. Prior to pupation burrows are formed at right angles to the larval burrows and out to the inner surface of the bark. This burrow is plugged with frass and pupation takes place at the angle in the burrow. Transformation occurs in the fall and emergence in the spring. Mortality between transformation and emergence is very high, particularly in oak, eucalyptus, and alder. Hardy and Preece in British Columbia found this mortality in the latter host to range from 15 to 75 per cent. Adults are active in midsummer and may be seen flying over the ground at a height of about two or three feet or depositing eggs at the base of a tree or stumps. In British Columbia adults are commonly found on *Verbascum* (G. Stace Smith).

Genus **Ulochaetes** LeConte

Ulochaetes LeConte, 1854, Proc. Acad. Nat. Sci. Phila., 1854: 82; LeConte, 1857, Rep. Expl. Surv. Miss. Riv. to Pac., 12 (2): 62; Thomson, 1860, Class. Ceramb., p. 146; Thomson, 1864, Systema Ceramb., p. 411; Lacordaire, 1869, Genera Coleopt., 8: 478; Leng, 1890, Entom. Amer., 6: 12.

Form elongate, robust, subcylindrical; integument hairy. Head moderately broad; antennal tubercles not prominent; antennae filiform and longer than the body in the male, shorter than the body and with outer segments expanded in female, fifth segment as long as third and

fourth together; palpi with ultimate segment cylindrical. Pronotum dilated at sides, wider than long, densely hairy. Elytra shorter than metathorax, together wider than long, apices dehiscent, not reflexed. Legs moderately elongate; posterior tibiae straight or feebly sinuate. Abdomen broad at base, gradually narrowed apically in female, thickened apically in male.

Genotype: *Ulochaetes leoninus* LeConte.

Ulochaetes differs from *Necydalis* in the robust body form, hairy pronotum, short third and fourth antennal segments, and cylindrical last segment of the palpi. The following is the only known species of the genus.

Ulochaetes leoninus LeConte

Ulochaetes leoninus LeConte, 1854, Proc. Acad. Nat. Sci. Phila., 1854: 82; LeConte, 1857, Rep. Expl. Surv. Miss. Riv. to Pac., 12 (2): 62, Pl. 2, f. 12; Horn, 1867, Proc. Ent. Soc. Phila., 6: 293 (habits); Leng, 1890, Entom. Amer., 6: 12; Craighead, 1923, Bull. Can. Dept. Agr., (n. s.) 27: 83 (larva); Hardy and Preece, 1926, Pan-Pac. Ent., 3: 36 (habits); Hardy, 1926, Rep. Prov. Mus. Nat. Hist. B. C., 1925: 30, Pl. 5, f. 34.

Color black, apical one-third of elytra, and tibiae, except apices, testaceous; integument moderately shining. *Head* only moderately constricted behind eyes; surface densely, variably punctured, clothed with fine, erect, golden pubescence; vertex distinctly grooved, surface with coarse and fine punctures intermixed, the latter predominating; frons punctured similarly to vertex; antennal tubercles, viewed from front, obtuse at apices; antennae slender in male with segments six to eleven subequal in length and the ultimate segment longer than fourth and fifth together, robust in female with segments six to eleven rapidly diminishing in length, expanded, and ultimate segment shorter than fourth segment. *Pronotum* with a conspicuous but obtuse lateral tubercle; dorsal surface opaque, densely clothed with long, erect, ochreous hairs which obscure the surface; scutellum shining, sides hairy; metasternum and metepisterna moderately finely, closely punctured, shining, subglabrous. *Elytra* nearly plane but with a feeble, transverse, subapical impression; disk opaque, apices and lateral margin somewhat shining; surface subglabrous, punctation fine and dense on disk, sparser apically, coarser in humeral region; apices dehiscing suddenly from middle, inner apical angle acute, apices separated by much more than their widths. *Legs* shining, sparsely pubescent; femora moderately densely punctured; tarsi moderately slender, first segment less than twice as long as following two together, about as long as following three together. *Abdomen* shining, sternites finely and very closely punctured, subglabrous.

Type locality: Prairie Pass, Oregon.

Distribution: Pacific Coast from British Columbia to mountains of southern California.

Hosts: *Pinus, Pseudotsuga, Picea, Abies.*

Ulochaetes leoninus bores in the heart and sapwood of a variety of conifers but most commonly in *Pinus ponderosa* and

Pseudotsuga taxifolia. The adults lay their eggs at the base of standing dead trees or stumps and the larvae are usually root feeders. Frequently, however, they bore in the basal six r eight feet of the main trunk. Like *Necydalis* they usually bore with the grain, turn at right angles prior to pupation and plug the emergence burrow with frass. Root-feeding larvae usually emerge above ground near the base of the tree. The females fly with a loud buzzing sound and keep the tip of the abdomen curved forward over the dorsum while in flight. They are most active in late summer and fly about in mid-morning and mid-afternoon. Males are rarely captured in flight but are often predominant in the host.

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ADDITIONAL NOTES ON PTEROCHEILUS DIVERSICOLOR ROHWER (HYMEN: VESPIDAE)

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In my recent revision[1] of the genus *Pterocheilus* Klug the description of the species *diversicolor* Rohwer was inadvertently left out although it appeared in the keys to both sexes. It belongs to the subgenus *Micropterocheilus* Bohart and is easily distinguished by its red and white markings, small size, and truncate clypeus.

Pterocheilus (Micropterocheilus) diversicolor Rohwer

Pterochilus diversicolor Rohwer, 1911. Proc. U. S. Nat. Mus., 40: 554 (holotype female, U. S. N. M.).

Male.—Head and thorax black with orange-yellow markings, antenna orange-red, legs orange-yellow, abdomen black at base of first two segments but otherwise orange-red except for white apical bands on first six tergites and second sternite; wings yellowish anteriorly. Pubescence pale and obscure except on vertex and front where it is sparse and about four ocellus lengths. Puncturation moderately coarse and close, fine and sparse on clypeus. Clypeus octagonal, latero-apical sides the longest; last antennal segment rounded apically; middle femur not depressed beneath at base; length to apex of second tergite 7.5 mm.

Female.—Markings, pubescence, and puncturation about as in male except as follows: Body mostly orange-red, edged with black in places; first four tergites apically white banded. Mandible very slender and with teeth hardly indented; clypeus truncate apically, the corners rounded; length to apex of second tergite 8 mm.

Records (all from California). Holotype female, San Diego Co. (D. W. Coquillett); two males and three females, Thousand Palms, Riverside Co., March (E. G. Linsley and R. M. Bohart); one male and one female, Olancha, Inyo Co., May 20, 1937 (F. L. Blanc).

[1]Bohart, R. M., A Revision of the North American Species of the Genus Pterocheilus and Notes on Related Genera. Ann. Ent. Soc. Amer., 33: 162–208, 1940.

A REVISION OF THE PIMPLINI OF EASTERN NORTH AMERICA

(Hymenoptera, Ichneumonidae)

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The Ichneumonidae included in this paper are of the subfamily Pimplinae and constitute the tribes Pimplini (=Ephialtini)[1] and Theroniini of Cushman and Rohwer. Being typical pimplines, the petiole is short and broad with its sternum not fused with the tergum and the spiracles at or before its midlength. The areolet is more or less triangular and the ovipositor exserted. These latter two characters are subject to rare exceptions. The genera treated here differ from other Pimplinae in having *either* the mesopleural suture nearly straight, without the usual sharp bend near its middle *or* the tarsal claws very large and strong with a large pocket on the mesal side of each and usually also with a large specialized hair that is flattened and curved at the tip (fig. 8). Some genera possess both of these characters. In addition, this group of genera has a robust build, the nervulus broken high above the middle, and the female subgenital plate not strongly developed. The ovipositor is stout, about half as long as the abdomen and has a series of ridges at the end. It may rarely, however, be slightly longer than the abdomen or so short as not to surpass its tip.[2]

The species of Pimplini included are those occurring in the Nearctic Region east of the Mississippi River, the Great Lakes and Hudson Bay.

Cushman[3] has already published a revision of the Nearctic species of the present genera. His papers have made identification of the species easier and more certain and I have used them as the basis for my own work. He has, however, left unclarified certain species of *Apechthis* and *Pimpla*. *Apechthis annulicornis* and *A. picticornis* are in the present paper shown to be distinct species, while *Pimpla aquilonia* is here more

[1]See under the genus *Pimpla* for a discussion of nomenclature.

[2]In the Cornell University Collection is a species of *Theronia* from Peru with the ovipositor so short as not to exceed the tip of the abdomen. In other respects it is of the normal Neotropical type of *Theronia*.

[3]Proc. U. S. Nat. Mus. 1920 58: 38–45, 327–362.

clearly distinguished from *P. aequalis* and *P. tenuicornis*, and two new species of *Pimpla* resembling the above three are described as new. In order to point out the distinctions between these species and incidently to add other observations, the present revision was undertaken.

This study is based largely upon my own collection (Townes) and that of Cornell University (Cornell). Other material studied is in the collections of the United States National Museum (U. S.), Mr. R. R. Dreisbach of Midland, Michigan (Dreisbach), and several smaller collections. Following the names of the collections in the parentheses are the abbreviations used in this paper. I have examined and compared specimens with all of the pertinent types of Cresson (except *Pimpla bicincta* and *P. tolteca*), Provancher, Viereck, and Davis. The types of *Ichneumon hilaris* Say and *Pimpla petiolatus* Say are lost and neotypes are designated in this paper.

My wife has given assistance by getting the distributional data together, making the drawings, and typing the manuscript. Also, she has collected much of the material. Mr. R. A. Cushman, Prof. J. Chester Bradley, and Mr. J. F. Perkins have read the manuscript and have saved me from many errors. Mr. Cushman has obligingly secured the loan of material from the United States National Museum that included representatives of several species I would not otherwise have been able to study, and has supplied distributional data from specimens in the National Museum. Dr. W. T. M. Forbes has helped me with the synonymy of the Lepidoptera recorded as hosts.

Cushman and Rohwer[4] have divided the present group of genera into two tribes, the Ephialtini (=Pimplini) and the Theroniini. *Theronia* is placed in the Theroniini and the rest in Ephialtini, though *Lissopimpla* is not actually mentioned. As tribal characters they state that the Theroniini have the propodeal spiracle separated from the base of the propodeum by less than its length, the notauli subparallel and ending abruptly, the propodeal carinae strong, the abdomen polished, and the dorsal margin of the ovipositor straight to the apex; the Ephialtini are said to have the propodeal spiracle separated from the base of the propodeum by more than its length, the notauli obsolete or converging, the propodeal carinae strong, the abdomen punctate, and the dorsal margin of the ovipositor decurved

[4]Proc. U. S. Nat. Mus. 1920 57: 389, 392, 394.

or flattened at the apex. These authors based their tribal division partially on larval characters, but have not described the differences they found. Except that the larval head capsule of *Theronia* is distinctly different from that of *Pimpla*, *Itoplectis*, *Xanthopimpla*, and *Echthromorpha* I am not familiar with the larval characters known to Cushman and Rohwer.

I have studied the adult characters enumerated by Cushman and Rohwer and all others which might support their tribal division. It seems to me that on adult characters *Theronia* can not be put in a separate tribe because it has the same habitus as the rest of the genera and I can find no single reliable character by which it differs from them. Since *Theronia* is similar to these genera in life history also, I feel justified in placing them all in the one tribe Pimplini. The tribe may be recognized by the characters and habitus described in the first paragraph. Unfortunately it is difficult to define the Pimplini clearly and I am not sure but that the tribal limits will subsequently have to be changed to include such genera as *Perithous* and *Delomerista*, which show many of the characteristics of this group.

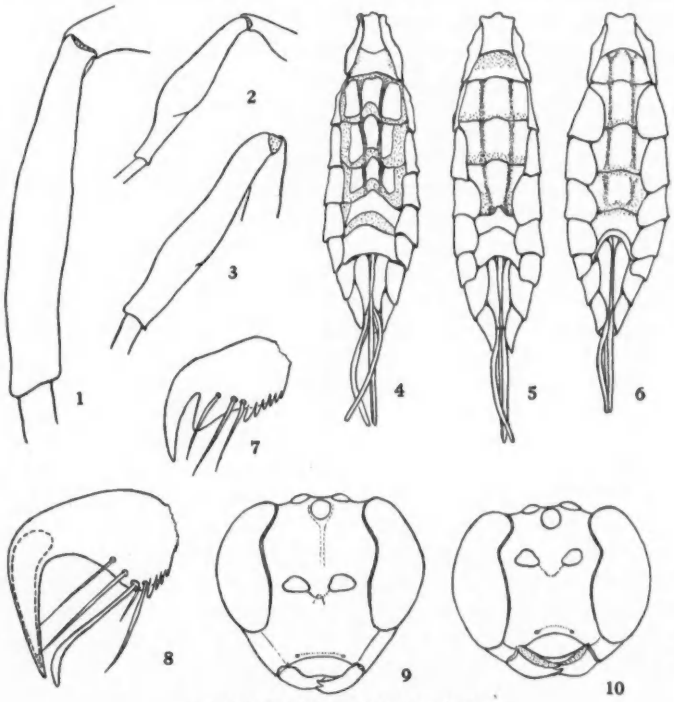
The genera fall into three series. *Xanthopimpla*, *Echthromorpha*, and *Lissopimpla* are a group of the Old World Tropics except for a few species of *Xanthopimpla* in Central and South America. *Echthromorpha* and *Lissopimpla* are especially closely related. *Theronia* belongs in a group by itself. *Pimpla*, *Apechthis*, and *Itoplectis* form the third group with *Apechthis* and *Itoplectis* being the most closely related. The key to genera is a natural one and summarizes the characters of the generic groups.

Pimpla, *Apechthis*, and *Echthromorpha* give off a strongly pungent odor when captured.[5] The species of *Itoplectis* and *Theronia* that I have collected are odorless.

The tarsal claws of the genera *Theronia*, *Xanthopimpla*, *Echthromorpha*, and *Lissopimpla* are of a peculiar and unusual type. The claw is very large, bent at a sharp right angle near its middle, and the apical half has a large pocket in its mesal side that occupies over half the length of this apical portion. (fig. 8). This pocket is broad at the base and tapers to a fine point at the tip. It is hollowed out of the claw itself and is covered with a membrane. Probably it is produced by the eccentric enlargement of the central cavity of the claw and the

[5]Townes: Bull. Brooklyn Ent. Soc. 1939 34: 29–30.
Williams: The Insects and other Invertebrates of Hawaiian Sugar Cane Fields 1931, p. 266.

covering membrane is the substance of the claw thinned out over the inner side of the pocket. The pocket contains a substance that upon drying looks either chalky or like transparent glue. Since the deepest part of the pocket (the broad base) is at the sharp bend in the claw, this point is quite weak and the



DESCRIPTION OF FIGURES

Fig. 1.—*Pimpla pedalis* Cress., front tibia of female. 2.—*Pimpla inflata* n. sp., front tibia of female. 3.—*Pimpla nuda* n. sp., front tibia of female. 4.—*Pimpla aquilonia* Cress., underside of female abdomen. 5.—*Pimpla tenuicornis* Cress., underside of female abdomen. 6.—*Pimpla aequalis* Prov., underside of female abdomen. 7.—*Itoplectis conquisitor* Say, front tarsal claw of female. 8.—*Theronia atalantae* Poda, middle tarsal claw of female. 9.—*Pimpla pedalis* Cress., face of female. 10.—*Itoplectis conquisitor* Say, face of female.

claw is easily broken here. When one of these insects is caught in a net, it clings tenaciously to the cloth with its long claws. If it is removed roughly, several claws are usually broken during the process. Correlated with the large claws is a long strong planta. This is evidently an adaptation to allow the insect to disengage its claws by depressing the planta at the same time

that it retracts the claws. There is another specialization provided, apparently, to keep the claws from being sunk too deeply except upon certain occasions. The ungual bristles are long and stout and in all except *Lissopimpla*, the last bristle is exceptionally large with a flattened curved tip that in its normal position is fitted against the point of the claw as if to sheath it. It is difficult to explain these many curious modifications of the tarsal claws. The most likely explanation is that they are specialized as organs for defense. When seized by a predator they may sink the claws into the delicate skin and when torn loose the tips of some of the claws may then break off in the skin. Breaking off the claw tip would tear open the pocket in it and allow its perhaps poisonous contents to cause irritation or severe poisoning. If these suppositions prove correct, there will also be provided an explanation for the bright colors of most of these insects and the fact that they seem to serve as models for mimicry.

All other genera of the group under discussion have rudiments of these specializations. The claws of all are quite large with long stout ungual bristles showing a tendency to become flattened and curved at the tip as in *Theronia*, *Xanthopimpla*, and *Echthromorpha*. In species of *Pimpla* and *Itoplectis* having unusually large claws, it is even possible to see a small pocket. The claws of the entire group are not simple, as usually stated, but have at the base a few small teeth (figs. 7 and 8) even in those genera in which the female has a large tooth on the claw (*Itoplectis* and *Apechthis*). The importance of these ungual characters is lessened because they are not entirely restricted to the group of genera under discussion. Strong ungual bristles are present on nearly all unusually large claws, the small teeth are present at the base of most claws that appear simple, and the pocket occurs in rudimentary form in *Perithous* and perhaps in other genera.

Members of the tribe Pimplini, as here defined, are all parasitic upon Lepidoptera. Each species parasitizes a variety of hosts differing greatly both in size and in relationships. Oviposition is into prepupae or into freshly formed pupae that may be entirely naked or enclosed in a dense cocoon, but subterranean pupae or those well protected in burrows in twigs or weeds are not attacked. Species of *Pimpla* are known occasionally to parasitize active larvae. Some species of Pimplini, especially those of *Theronia* and *Itoplectis*, are often secondary parasites, usually upon the larvae of other Pimplini. The parasite larva

develops as a solitary internal parasite in the host pupa. If it is a secondary parasite, it is external to the secondary host but internal to the primary host. The larva matures in a few weeks and spins a few strands of silk as a flimsy cocoon within the lepidopterous pupa. The adult emerges through a hole gnawed in the anterior end of the pupa. The adult parasite varies in size with that of its host. Males are usually smaller than and outnumber the females. It has been shown that the males usually develop from smaller hosts and females from larger hosts.[6] In the northeastern United States, all species of the tribe appear to have two broods (and probably a partial third) and to overwinter in the host pupa, though overwintering adult females of *Theronia atalantae* have been found. Adults may be found throughout the growing season, but only females are common in the fall.

The following key includes all of the genera of Pimplini known to me. Many other genera have been referred to the tribe, but all, of which I have seen specimens, belong elsewhere.

KEY TO THE GENERA OF PIMPLINI

1. Labrum exposed, plate-like, in about the same plane as the clypeus; mandibles tapering to a narrower tip and with the lower tooth decidedly shorter than the upper. (exotic genera).....2
   Labrum normally concealed when the mandibles are closed, somewhat inside the plane of the clypeus; mandibles broad at the tip and with the lower tooth not decidedly smaller than the upper.....4
2. Tip of mandible turned 90° so that the lower tooth is inward; propodeum polished and usually with strong carinae; nervellus broken at about its upper 0.25. (tropical regions).....**Xanthopimpla** Saussure
   Tip of mandible not or only slightly turned; propodeum punctate, striate, or mat and without carinae; nervellus broken at its upper 0.15 or above, sometimes the discoidella arising from the cubitella near the nervellus.....3
3. Hind femur with a small acute tooth beneath near the tip; abdomen polished; nervulus interstitial to antefurcal. (Oriental and Australian regions), **Lissopimpla** Kriechbaumer
   Hind femur without a tooth; abdomen punctate or somewhat mat, not polished; nervulus strongly postfurcal. (Old World tropics), **Echthromorpha** Holmgren[7]

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[6]Clausen has discussed this phenomenon (J. New York Ent. Soc. 1939. 47: 1–9.)

[7]I have seen the types of *Allotheronia* 12-*guttata* Ashmead and of *Glyptogastra hawaiiensis* Ashmead at the U. S. National Museum. These are the genotypes of *Allotheronia* and *Glyptogastra* respectively. Both are simply aberrant species of *Echthromorpha* and though they might be useful as subgenera should not be held as distinct genera (new synonymies). The type of *Allotheronia* 12-*guttata* is a specimen of *Echthromorpha intricatoria* Fabricius (new synonymy) which differs from typical *Echthromorpha* in having a pair of prominent tubercles on the propodeum and the propodeum closely punctate. *Echthromorpha hawaiiensis* (new combination) differs from typical *Echthromorpha* in having the petiole longer than usual with a prominent dorsal hump behind the middle. Also the nervellus is broken at about its upper 0.12, the malar space is short, and the abdomen is practically impunctate. Probably *Habropimpla* Cameron will prove to be a synonym of *Echthromorpha*. Except for the alleged fact that the two teeth of the mandible are of the same size, the characters given by Cameron and by Morley for *Habropimpla* fit *Echthromorpha* very well.

4. Abdomen completely polished and impunctate; propodeum polished and usually with strong carinae; tarsal claws very large and with a large "poison pocket" (fig. 8)..... **Theronia** Holmgren
   Abdomen more or less punctate or mat; propodeum more or less punctate or striate and rarely with strong carinae; tarsal claws only moderately large and without a large "poison pocket"..... 5
5. Eye weakly emarginate above antenna (fig. 9); face of male black; tarsal claws of female without a tooth (except for microscopic teeth at the extreme base)..... **Pimpla** Fabricius
   Eye sharply and strongly emarginate opposite antenna (fig. 10); face of male white, yellow, or black; front tarsal claws of female usually with a large tooth (fig. 7)..... 6
6. Ovipositor hooked downward at tip; face of male white or yellow or largely so; orbits of female in front narrowly whitish..... **Apechthis** Foerster
   Ovipositor straight; face and orbits of both sexes entirely black (at least in the Nearctic species)..... **Itoplectis** Foerster

Genus **Theronia** Holmgren

Theronia Holmgren, Oefvers Vet.-Acad. Forh. 1859. 16: 123. Genotype: (*Pimpla flavicans* Fab.) = *Ichneumon atalantae* Poda.
Pseudacoenites Kriechbaumer, Ent. Nachr. 1892. p. 219. Genotype: (*Pseudacoenites moravicus* Kriech.) = *Theronia laevigata* Tscheck.
Neotheronia Krieger, Sitz. naturf. Ges. Leipzig, 1898. p. 119, n. syn. Genotype: *Theronia tolteca* Cresson.
Epimecoideus Ashmead, Proc. U. S. Nat. Mus. 1900. 23: 52, n. syn. Genotype: *Epimecoideus apicalis* Ashmead.
Erythrotheronia Cameron, Spolia Zeylanica. 1905. p. 34, n. syn. Genotype: *Erythrotheronia flaviolineata* Cameron.
Orientotheronia Morley, Ich. Brit. India. 1913. 1: 146. Genotype: *Orientotheronia rufescens* Morley.

The genus *Theronia* is easily distinguished by its polished impunctate abdomen, polished carinate propodeum, and very large tarsal claws each with a pocket on the inner side and each with a large specialized hair which is flattened and curved at the tip (fig. 8). The Nearctic species all have a yellow or ferruginous ground color. All other species treated in this paper are mostly black. The shape of the penis seems to give good characters for separating Neotropical species of this genus and should be investigated by anyone doing revisional work among them.

Various species of *Theronia* differ markedly in the course and strength of the propodeal carinae and of the prepectal carina. Species from the same region often show relationship by having rather similar carinae. This has contributed to the erection of several genera based mainly on propodeal characters. *Neotheronia* of the Neotropical region is defined as having a strong transverse carina on the propodeum with the other propodeal carinae weaker and as having the apex of the fore wing infumate. Although the majority of Neotropical species conform to this general pattern, others are intermediate to the Holarctic type (typical *Theronia*) in which the wings are unicolorous and the propodeum is rather completely areolated with

all carinae of about equal strength. Many of the Neotropical species placed by Krieger in his genus *Neotheronia* do not differ from typical *Theronia* at all. Cushman[8] recognized *Epimecoideus* Ashmead as related to *Neotheronia* and recorded characters by which the two genera might be distinguished. His characters are apparently based upon the comparison of the two species, *Epimecoideus apicalis* Ashmead and *Neotheronia septemtrionalis* Krieger. When other species are examined, each of Cushman's characters is seen to be of no generic importance. Morley's *Orientotheronia* was erected for species having the transverse propodeal carina weak or absent in the middle. Species having this character are common in the Old World tropics. Other species from the same regions show all intergrades between typical *Orientotheronia* and typical *Theronia*. Cameron's *Erythrotheronia* apparently does not differ from typical *Theronia* in any fundamental way. Cameron erected it as a new genus because it had simple tarsal claws, while Ashmead had stated (erroneously) that the claws of *Theronia* are pectinate. Mr. J. F. Perkins of the British Museum has examined the types of *Erythrotheronia flavolineata* Cameron and of *Orientotheronia rufescens* Morley and reports to me that they are both species of *Theronia*. For these reasons it seems inadvisable to hold *Neotheronia*, *Epimecoideus*, *Erythrotheronia*, and *Orientotheronia* as genera distinct from *Theronia*. Perhaps further study will show that *Theronia* can be divided into subgenera for which some of the names discarded above may be used.

KEY TO SPECIES OF THERONIA OF EASTERN NORTH AMERICA

1. Fore wing with a definite dark spot near the apex; propodeum with a transverse carina across its middle and no carinae basad of the transverse carina, **septemtrionalis**
   Fore wing without a definite dark spot near the apex; propodeum with a less regular transverse carina across its middle and with definite carinae above the transverse carina.....2
2. Head almost entirely black; body ferruginous.....**hilaris**
   Head mostly ferruginous or yellow.....3
3. Hind femur beneath sharp for a part of its length and in all except small specimens with a weak irregularly serrate carina; lateral carinae on basal half of propodeum strong; abdomen rather uniformly ferruginous.....**atalantae**
   Hind femur rounded beneath; lateral carinae on basal half of propodeum weak or absent; basal three segments of abdomen yellow at apex with a broad brownish band across the base.....**bicincta**

Theronia septemtrionalis Krieger

Neotheronia septemtrionalis Krieger, Zeitschr. Hym. Dipt. 1905. 5: 305 ♂.
Neotheronia winnamanae Viereck, Proc. U. S. Nat. Mus. 1913. 44: 567 ♀, n. syn.
Neotheronia winnamanae Cushman, Proc. U. S. Nat. Mus. 1920. 58: 44.

[8]Proc. U. S. Nat. Mus. 1920. 58: 39, 40, 44.

Neotheronia septemtrionalis Cushman, Proc. U. S. Nat. Mus. 1920. 58: 45.
Neotheronia septemtrionalis Brimley, Ins. N. Car. 1938. p. 409.
Neotheronia winnamanae Brimley, Ins. N. Car. 1938. p. 409.

In his description of *septemtrionalis*, Krieger does not mention a dark band across the middle of the petiole, but this was apparently an oversight as the present species fits his description in every other particular.

Female.—Wing 8.5–11 mm. Lemon yellow, the top part of head, hind legs, tarsi, and apical part of abdomen somewhat suffused with orange. Blackish markings as follows: three long stripes on mesonotum; a short narrow one above tegula; groove at base of scutellum; a stripe across base of propodeum and in front of spiracles; a spot on fore wing about the tip of radial vein (wings otherwise hyaline); last two segments of hind tarsus except beneath; extreme base of petiole and a stripe across its middle; and a subbasal transverse stripe on tergites 2–6 occupying about one fourth of the length of the tergite. The yellow ground color is easily changed by cyanogen into an orange red.

Apical edge of clypeus convex; prepectal carina near its upper end bending sharply forward to reach nearly to the pronotum; scutellum with high carinae at its extreme base which abruptly fade out; metapleurum separated from propodeum by a complete carina; propodeum with a strong evenly curved transverse carina across its middle; both sets of carinae between the transverse carina and the base of propodeum obsolete; petiolar area bounded laterally by a strong but blunt carina at the summit of which the transverse carina is somewhat stronger than at its center; petiole about 2.1 as long as wide at apex, its dorsal carinae fading out before the spiracles; ovipositor sheath about as long as hind femur.

Male.—Similar to female except for the usual sexual differences.

Material: ♂, 13 ♀ from N. C. (Murfreesboro), S. C. (Greenville and Calahan Mt. in Greenville Co. at 1,100 ft.), Tenn. (Smoky Mountains), and Mo. (Willard). Cushman has recorded specimens from Md. (Plummer's Island and Cabin John), Ala. (Pyziton and Coleta), and La. (Tallulah). Brimley records the species from Raleigh and Marion, N. C.

This species is widely distributed in the Upper and Lower Austral zones of the Southeastern States. Like other species of its genus it flies low to the ground in the undergrowth of woods. The dark markings are then not visible and it is seen as a pale yellow streak.

Theronia hilaris Say

Ichneumon hilaris Say, Contrib. McClur. Lyc. Phila. 1829. 1: 71 ♂.
Pimpla melanocephala Brullé, Hist. Nat. Ins., Hym. 1846. 4: 99 ♀. (not Gravenhorst), n. syn.
Ichneumon hilaris Leconte, Writ. of Th. Say Ent. 1859. 1: 376.
Pimpla melanocephala Walsh, Trans. Acad. Sc. St. Louis. 1873. 1: 131.

Theronia melanocephala Cresson, Trans. Acad. Sc. St. Louis. 1873. 1: 132, note.
Theronia melanocephala Provancher, Addit. faune Canada Hym. 1889. p. 114.
Theronia melanocephala Krieger, Zeit. Hym. Dipt. 1906. 6: 233.
Theronia melanocephala Morley, Rev. Ich. Brit. Mus. 1914. 3: 40.
Theronia melanocephala Viereck, Hym. Conn. 1916. p. 323.
Theronia melanocephala Cushman, Proc. U. S. Nat. Mus. 1920. 58: 43.
Theronia ? hilaris Cushman and Gahan, Proc. Ent. Soc. Wash. 1921. 23: 165.
Theronia melanocephala Cushman, *in* Leonard: List Ins. N. Y. 1928. p. 936.
Theronia melanocephala Brimley, Ins. of N. Car. 1938. p. 409.

Since Say's type is lost, a neotype (♂, Poughkeepsie, N. Y., VII–30–36, H. K. Townes) is hereby established. It is now in the author's collection. Cushman and Gahan considered *Ichneumon hilaris* preoccupied by Gravenhorst. Say's name was published in January, 1829 (according to Sherborn) while the preface to *Ichneumonologica Europaea*, where *Ichneumon hilaris* Gravenhorst was first published, is dated March 19, 1829.

Female.—Wing 6.5–11 mm. Ferruginous, black as follows: head except more or less of clypeus and center of face; antenna except scape and pedicel beneath; usually stains on the propleurum and sides of the pronotum; and last two segments of hind tarsus except beneath. Wings hyaline with a slightly dusky tinge. Ovipositor sheath black.

Apical edge of clypeus emarginate; prepectal carina near its upper end curving sharply forward and nearly reaching pronotum; scutellum with high carinae at its extreme base which abruptly fade out; metapleurum separated from propodeum by a complete carina; median and lateral propodeal carinae present and complete; all propodeal carinae of approximately the same strength except for a very weak carina separating the external from the dentiparal area; petiolar area quite regularly hexagonal; petiole about 1.6 as long as wide at apex, its dorsal carinae strong to its apical fifth; ovipositor sheath about 1.4 as long as hind femur.

Male.—Similar to female except that the black markings have a tendency to be less extensive. Usually the male has a larger ferruginous area in the center of the face than the female.

Material: 125 ♂, 58 ♀ from Que. (Montreal); Me. (South Portland), Mass. (South Hadley), R. I. (Westerly), N. Y. (Bemus Point, Connecticut Hill, Downsville, Farmingdale, Hancock, Ithaca, Lake George, McLean, Millwood, New Russia, Olcott, Oneonta, Oswego, Poughkeepsie, Rock City, Shokan, Slide Mt. 2,800–4,000 ft., Syracuse, and Troy); Mich. (Alcona Co. and Midland Co.), Pa. (Buena Vista, Chaffee, Enola, and Lehigh Gap), Md. (Perry Hall); N. C. (Swannanoa 3,000 ft. and Waynesville), N. J. (Moorestown), and S. C. (Greenville Co.). Viereck records this species from Portland, Conn. Cushman records it from the additional states of Ind., W. Va., and Va.; Provancher records it from Ottawa, Ont.; and Brimley records it from the additional N. C. localities of Grandfather Mt.,

Pineola, and Raleigh. The type of *hilaris* (lost) is from Indiana and that of *melanocephala* from "North America."

This species seems to be restricted to the Transitional and Upper Austral zones east of the Mississippi River. In the Northeastern States it is abundant. I have personally collected in thirteen of the nineteen New York localities recorded and found it common at each. Its characteristic habitat is dense deciduous woods with comparatively little undergrowth, a situation preferred by relatively few species of ichneumons. It is, however, also abundant in dense undergrowth. It usually flies within six inches of the leaf mold. Collection dates range from May 23 at Ithaca, N. Y., to October 10 at South Hadley, Mass. In central New York during the last part of May and the first half of June, females are scarce but small male specimens are abundant. Females are less common than males until about July 15, after which they are about as common. Males are scarce after September 1, though females occur in some numbers till October. It seems probable that this species has two and possibly three generations per season in central New York. It has been recorded as a parasite of *Lymantria dispar*, *Malacosoma americana* (associated with *Pimpla pedalis*), *Halisidota maculata*, and *Epargyreus tityrus*. *Theronia atalantae* is a very common parasite of *Lymantria dispar* and *Malacosoma americana*. It is believed that the records of *T. hilaris* from these hosts are due to misdetermination of *T. atalantae*.

Theronia atalantae Poda

Ichneumon atalantae Poda, Insect. mus. graec. 1761. p. 106.
Ichneumon flavicans Fabricius, Entom. System. 1793. 2: 182.
Theronia flavicans Holmgren, Oefvers Svensk. Vet.-Akad. Forhandl. 1859. 6: 123.
Pimpla fulvescens Cresson, Proc. Ent. Soc. Phila. 1865. 4: 268.
Pimpla sp. near *melanocephala* Walsh, Practical Entomol. 1867. 2: 116.
Pimpla sp. near *melanocephala* Riley, Ann. Rep. Ins. Mo. 1871. 3: 129.
Theronia fulvescens Howard, U. S. Dept. Agr. Bur. Ent. Tech. Bull. 1897. 5: 24.
Theronia atalantae Krieger, Sitzber. naturf. Ges. Leipzig. 1899. p. 113.
Theronia atalantae Dalla Torre, Cat. Hymen. 1901. 3: 463–465.
Theronia fulvescens, var. *mellipennis* Viereck, Trans. Amer. Ent. Soc. 1903. 29: 87, n. syn.
Theronia fulvescens Fiske, N. H. Coll. Agr. Exp. Sta. Tech. Bull. 1903. 6: 217.
Theronia atalantae var. *americana* Kreiger, Zeitschr. Hym. Dipt. 1906. 6: 240.
Theronia japonica Ashmead, Proc. U. S. Nat. Mus. 1906. 30: 181.
Theronia fulvescens Fiske and Thompson, J. Econ. Ent. 1909. 2: 455–457.
Theronia fulvescens Howard and Fiske, U. S. Dept. Agr. Bull. 1911. 91: 137, 144, 236–237.
Theronia fulvescens Aldrich, J. Econ. Ent. 1912. 87–88.
Theronia fulvescens Morley, Rev. Ichn. Brit. Mus. 1914. 30: 40.
Theronia atalantae fulvescens Viereck, Hymen. Conn. 1916. p. 323.
Theronia fulvescens fulvescens Cushman, Proc. U. S. Nat. Mus. 1920. 58: 40–42.
Theronia fulvescens mellipennis Cushman, Proc. U. S. Nat. Mus. 1920. 58: 41, 43.
Theronia atalantae Uchida, J. Fac. Agric. Hokkaido Imp. Univ. 1928. 25: 40.

The American synonymy is given above in full, but only the more important papers on biology are cited. Of the many European and Japanese references only the important synonymy is listed. Complete synonymy up to 1900 may be found in Dalla Torre's *Catalogus Hymenopterorum*. Besides the specific names listed above, this species has gone under the following in Europe: *acuminator*, *albiscutatus*, *colonator*, *crassipes*, *incisus*, *melanops*, *nigroculus*, *quadripunctatus*, *scutellatus*, *speculator*, *superbus*, *variatorius*, *varius*, *vinctus*, and *vulpes*. Until 1899 it was commonly called *flavicans* and since then has been called *atalantae*.

Female.—Wing 9–12 mm. Tawny with rather indefinite yellow markings on head, thorax, and legs. The more definite of the yellow markings are on the face, mesopleurum just below tegula, scutellum, metanotum, and knee of the middle leg. Flagellum brown, prepectus near lower angle of the pronotum blackish, and ovipositor sheath black. This is the typical form of North America. European specimens on the average have a darker ground color and more dark markings. Japanese specimens are the darkest of all. Both dark and light specimens, however, occur in all localities. I have a specimen from Shokan, N. Y., as dark as Japanese specimens. It is mottled with dusky brown blotches, the more conspicuous of which are as follows: occiput; most of thorax except the places customarily yellowish (darkest along the sutures); hind coxa; and basal third of abdominal tergites. Dark markings are most likely to occur in these places but their exact distribution is somewhat variable.

Apical edge of clypeus slightly emarginate; prepectal carina roundly curved forward almost reaching pronotum; scutellum not carinate laterally; metapleurum separated from propodeum by a complete carina; median and lateral propodeal carinae present, the latter usually fading out opposite spiracle; lateral section of transverse carina weak; petiolar area rather regularly hexagonal, the carina bounding it at the side stronger than others on the propodeum; apical half of hind femur beneath with a ridge which bears in all but the smallest specimens several blunt teeth, a character shared with no other species of the genus; petiole about 1.5 as long as wide at the apex, its dorsal carinae strong to its apical third; ovipositor sheath 1.5 as long as hind femur.

Male.—Similar to female except for the usual sexual differences.

There seems to be nothing in either morphology or biology to distinguish the Nearctic from the Palaearctic individuals of this species. Until a tangible difference is demonstrated they should not be considered even subspecifically distinct. Those who would label American specimens *fulvescens* and European specimens *atalantae* should remember that specimens of *atalantae* from Europe have been liberated in our New England states as parasites of the gypsy moth. Neither does *mellipennis*

deserve subspecific recognition. Viereck based this name on a specimen from New Mexico with the face weakly striate. Specimens from any locality frequently show these striations.

Material: 56 ♂, 29 ♀ (in addition to 5 ♂ and 9 ♀ from Europe and Japan). My specimens are from Mass. (Princeton): R. I. (Westerly); N. Y. (Bemus Point, Farmingdale, Ithaca, Lake Mohonk, McLean, Poughkeepsie, Shokan, and Troy); N. J. (Moorestown and Palisades); Mich. (Alcona Co., Iosco Co., Midland Co.); N. Mex. (Jemez Springs, 6,400 ft.); Ariz. (Oak Creek Canyon 6,000 ft.); and Calif. (Muir Woods). Collection records are from June 2 to October 19 at Ithaca, N. Y. The type of *fulvescens* is from Colorado, that of *mellipennis* from Beulah, New Mexico, and that of *americana* from British Columbia. These and other published data give the species a range in North America from Ontario to Princeton, Mass. to Waccamaw Lake, N. C., to Oak Creek Canyon, Ariz., to Muir Woods, Calif., to British Columbia. It occurs all over Europe, Japan, Korea, Sachalin, Kurilin, and has been found in Siberia and the Amur region.

This species is not rare in the Transitional Zone of the Northeastern States. It occurs in rank undergrowth of woods. In some localities it is common, but it is more often scarce. According to Schmiedeknecht, this is also true in Europe.

Due partly to the fact that it is a parasite of the gypsy moth, brown-tail moth, and tent caterpillar, *T. atalantae* has been reared innumerable times and there are several good reports on its biology. Its known hosts are Psychidae (*Clania minuscula*), Tortricidae (*Archips fumiferana*, *Cnephasia bellana*, *Evetria resinana*, and *Tortrix viridana*), Pyralidae (*Loxostege verticalis*, *Phylctaenia forficalis*, and *Sylepta ruralis*), Thyatiridae (*Cymatophora octogesima*), Drepanidae (*Oreta rosea*), Geometridae (*Abraxas grossulariata* and *Ourapteryx maculicaudaria*), Lasiocampidae (*Dendrolimus albolineatus*, *D. spectabilis*, *D. pini*, *Malacosoma americana*, *M. disstria*, *M. neustria*, *M. neustria testacea*, and *M. sylvatica*) Saturnidae (*Callosamia promethea*), Lymantriidae (*Euproctis phaeorrhea*, *Hemerocampa leucostigma*, and *Lymantria dispar*), Noctudiae (*Agrotis fimbria*), Arctiidae (*Lithosia quadra*), Hesperiidae (*Parnara guttata*), Pieridae (*Neophasia menape* and *Pieris rapae*), and Nymphalidae (*Argynnis paphia*, *Limenitis sibylla*, *Vanessa atalanta*, *V. californica*, and *V. polychloros*). It has been shown to be a secondary parasite on Ichneumonidae (*Erematylus macrurus*, *Itoplectis con-*

quisitor, and *Spilocryptus nuncius*) and Tachinidae (*Nemorilla floralis*). A pteromalid, *Dibrachys boucheanus*, was reared as a parasite of *Theronia atalantae* by Fiske.

The most common hosts seem to be Lasiocampidae and Lymantriidae. It is the commonest pupal parasite of the gypsy moth and the brown-tail moth. In the case of the tent caterpillar (*Malacosoma americana*) it is almost invariably a secondary parasite, usually on *Itoplectis conquisitor*. On *Callosamia promethea* it is usually a secondary parasite of *Spilocryptus nuncius* or *Eremotylus macrurus*, though in a few cases it develops as a primary parasite. *Theronia* seems to have difficulty escaping from the tough cocoon of *Callosamia*, as adults are frequently found dead in the cocoon.

Aldrich reports that this parasite curbed an outbreak of *Neophasia menapia* in the Northwest. In the years 1896 to 1898, *Neophasia* caused much damage by defoliating pine and fir timber at Moscow, Idaho, and other sections of the Northwest. *Theronia atalantae* appeared. In 1898 it reached its maximum, in late summer swarming in the woods in unbelievable numbers. In places the air was so full of them that they made a humming like a swarm of bees. Specimens reared from *Neophasia* pupae were sent to the U. S. Bureau of Entomology for determination. The following spring, the extermination of *Neophasia* was complete all over the Northwest and Prof. Aldrich saw only one other specimen alive during the next ten years. The numbers of the parasite dropped to almost zero. No other parasite had been found common in the woods during this outbreak.

Theronia atalantae may be either a primary or a secondary parasite. If the host attacked has already been parasitized by another ichneumonid it becomes a secondary parasite, if not it lives as a primary. There is no clear evidence that it is obliged to be a secondary parasite on any host, although it has been shown usually to live thus in the case of *Malacosoma*. As a primary parasite the insect lives inside its host. When it is a secondary parasite it lives inside its primary host and outside of its secondary host. The egg is deposited only in a prepupa or a freshly formed pupa. Fiske believes the egg stage to last about a day. He has observed that on the average the first three larval stages last two days each and the fourth stage feeds for two days and then spins its cocoon for one day and rests two days before forming the pupa. After two to four days the pupa

hatches. Development from the egg to the adult thus consumes fourteen to eighteen days. When a secondary parasite on *Malacosoma americana* (through *Itoplectis conquisitor*) in New Hampshire, most of the adults emerged July 10–20, the females about four days behind the males. *Itoplectis conquisitor* emerged from the same cocoons on an average of seven days earlier than its parasite.

Theronia bicincta Cresson

Pimpla bicincta Cresson, Proc. Ent. Soc. Phila. 1865. 4: 38. ♀
Neotheronia bicincta Krieger, Zeitschr. Hym. Dipt. 1905. 5: 300.
Neotheronia bicincta Morley, Rev. Ichn. Brit. Mus. 1914. 3: 57.

Mr. H. P. Hopper has compared for me a specimen of this species with Cresson's type.

Female.—Wing 9–11 mm. Head yellow, a dusky band connecting lateral ocellus with eye; vertex with a ferruginous mark just above occipital carina; flagellum ferruginous. Thorax yellow, with three long dusky ferruginous stripes on mesonotum and black marks as follows: short line above tegula; groove at base of scutellum; area surrounding tip of metanotum; stripe on upper two-thirds of hind edge of pronotum; stripe along front edge at mesonotum; stripe extending from just above middle coxa to across base of propodeum; stripe along lower half of mesopleural suture; and a stripe along posterior edge of propodeum and metapleurum. Wings suffused with brownish orange, the tips slightly darker. Fore and middle legs yellow, slightly varied with orange. Hind legs ferruginous with trochanters, basal three tarsal segments, and upper and outer surfaces of the coxa yellow. First three abdominal tergites with the basal half brownish ferruginous and apical half yellow. Remaining tergites dark ferruginous. Ovipositor sheath yellow at base grading to black at apex.

Apical edge of the clypeus emarginate; prepectal carina obsolete above, but a trace of it curving forward toward the pronotum; scutellar carinae absent; metapleurum separated from the propodeum by a carina that fades out just before reaching the transverse carina; median carinae moderately strong and reaching base of propodeum; lateral carina vestigial; transverse carina moderately strong, dipped downward at juncture of strong carina bounding petiolar area laterally; petiole 2.0 as long as wide at apex, its dorsal carinae fading out just anterior to spiracle; ovipositor sheath about 1.25 as long as hind tibia.

Male.—Similar to female except for the usual sexual differences.

Material: ♀, St. Simons Is., Ga., VIII–31–30, P. W. Fattig (U. S.); ♀, Anastasia Is., St. Augustine, Fla., T. H. Hubbell (U. S.); ♀, Elfers, Fla., IV–5–37, J. G. Fanclemont (Townes); ♂, Gainesville, Fla., VI–31–25 (Townes); 4 ♂, Gainesville, Fla., emerged Feb., 1925, from spider egg sack containing *Tromatobia rufopectus*, W. A. Murrill (U. S.). The type was

described from Cuba and Morley states that a female in the British Museum is from the same locality.

This species appears to be fairly common in Florida.

Genus **Pimpla** Fabricius

Pimpla Fabricius, Syst. Piez. 1804. p. 112. Desirable genotype: *Ichneumon instigator* Fabricius.
Coccygomimus Saussure; *in* Grandidier, Histoire Phys. Nat. Polit. Madagascar. 1890. vol. 20, pl. XIV, fig. 12. ♀. Genotype: *Coccygomimus madecassus* Saussure.
Lissotheronia Cameron, Spolia Zeylanica. 1905. p. 139. Genotype: *Lissotheronia flavipes* Cameron.
Pimplidea Viereck, Bull. U. S. Nat. Mus. 1914. 83: 117. Genotype: *Pimpla pedalis* Cresson.
Ephialtes Cushman, (not Schrank, not Gravenhorst).
Opodactyla Seyrig, Mem. Acad. Malagache. 1932. 11: 60. Genotype: *Pimpla* (*Opodactyla*) *waterloti* Seyrig.

Both Morley[9] and Seyrig[10] have recorded their opinion that *Coccygomimus madecassus* is a species of *Pimpla*. The type of *Lissotheronia flavipes* has not been found at the British Museum. Morley[11] has synonymized his own *Pimpla ampla* with *Lissotheronia flavipes* and referred *flavipes* to *Pimpla*.

The generic name *Pimpla* is used here in its traditional sense. Viereck[12] has shown that the genotype of *Pimpla* is *Ichneumon manifestator* Linnaeus, a species of *Ephialtes* Gravenhorst. In the same paper Viereck showed that the type of *Ichneumon* is also *Ichneumon manifestator* Linnaeus. Thus the proper name for *Ephialtes* Gravenhorst is *Ichneumon* with *Pimpla* as a synonym (isogenotypic). Viereck therefore proposed the name *Pimplidea*, with *Pimpla pedalis* Cresson as genotype, for *Pimpla* of authors. Cushman and Rohwer[13] later showed that the name *Ephialtes* was first used not by Gravenhorst in 1829, but by Schrank in 1802, and that the genotype of *Ephialtes* Schrank (not Gravenhorst) is *Ichneumon compunctor* Linnaeus. Through an unfortunate misdetermination of the person who examined the type for them, Cushman and Rohwer believed *compunctor* Linnaeus to be the same as *Pimpla instigator* Fabricius and therefore that *Ephialtes* was the correct name for *Pimpla* of authors. Roman[14] examined the type of *Ichneumon compunctor* Linnaeus and found it to be the same as *Apechthis brassicariae* (Poda). Thus *Ephialtes* Schrank is the correct name for *Apechthis* Foerster (genotypes congeneric).

[9]Rev. Ichn. Brit. Mus. 1914. 3: 72.
[10]Mem. Acad. Malagache. 1932. 11: 60.
[11]Ann. Mag. Nat. Hist. 1914. 8th ser. 14: 408.
[12]Bull. U. S. Nat. Mus. 1914. 83: 117.
[13]Proc. Ent. Soc. Wash. 1918. 20: 186–188.
[14]Ent. Tidskrift. 1932. 53: 4.

In America the genus *Pimpla* of authors was called *Pimpla* until 1914, *Pimplidea* between 1914 and 1918, and *Ephialtes* from 1918 to date. *Ephialtes* correctly should be used for *Apechthis* and *Pimplidea* is antedated by *Coccygomimus* Saussure, which is the correct name for *Pimpla* of authors. To avoid further changes and confusion that will result from application of the rules of nomenclature, it seems best to use the names *Pimpla* and *Ephialtes* in their traditional senses.

The International Commission on Zoological Nomenclature has been requested to make *nomina conservanda* of *Pimpla* and *Ephialtes* with *Ichneumon instigator* Fabricius and *Ichneumon manifestator* Linnaeus as their respective genotypes. It has already voted to do this, but since it was neglected to publish the case a year before the vote was made, there remains the technical necessity to revote a year after publication. Publication was made soon after the first vote[15] but although the second vote may have been taken the results are still unpublished.

After studying all available species of *Pimpla*, I have come to the conclusion that the genus can be divided into subgenera upon epipleural characters (figs. 4, 5, and 6), supported by less definite characters in the propodeum and petiole. One subgenus, the largest, would include the species with narrow epipleura throughout (*maura*, *pedalis*, and *aquilonia* in our eastern fauna), another would include those with the second and third epipleura narrow and the fourth wider (*tenuicornis* and *sodalis* in the East), and the third subgenus would include the species with all epipleura wide (*aequalis*, *inflata*, and *nuda* in the East). I have not used subgeneric names in this paper because the matter needs a more thorough study and I do not know what names should be applied to the various subgenera, except that the subgenus *Pimpla* would include *tenuicornis* and *sodalis* and that the name *Pimplidea* applies strictly to *pedalis* and *aquilonia*.

KEY TO SPECIES OF PIMPLA OF EASTERN NORTH AMERICA

1. Middle and hind coxae and trochanters black 2
   Middle and hind coxae and trochanters ferruginous 3
2. All femora ferruginous, the tips more or less black ..... **sodalis**
   All femora black, the front and middle ones more or less white ..... **maura**
3. Posterior tibia entirely black ..... **pedalis**
   Posterior tibia black with a white annulus near the middle 4
4. Epipleurum of fourth segment more than 2.0 as long as wide (fig. 4); scape of male almost always with a white spot in front; dorsal longitudinal carinae of propodeum absent or indicated at the base as rounded ridges; abdomen mat and finely punctate ..... **aquilonia**

[15] Can. Ent. 1936. 68: 114.

Epipleurum of fourth segment of female (and usually of male) less than 2.0 as long as wide (figs. 5 and 6); scape of male entirely black; dorsal longitudinal carinae of propodeum present and sharp at the base; abdomen sub-polished and rather coarsely punctate.....5

5. Epipleurum of second segment very narrowly wedge-shaped, more than 4.0 as long as wide (fig. 5); tegula black.....**tenuicornis**

Epipleurum of second segment broadly wedge-shaped, not more than 3.0 as long as wide (fig. 6); tegula black, white, or brown.....6

6. Outer margin of hind tibia sparsely hairy, the hairs in places separated by more than their length; tegula black; wings slightly infuscate (male unknown).....**nuda**

Outer margin of hind tibia closely hairy, the hairs separated by less than their own length and not sparser than on the rest of the tibia; tegula white or brown and white; wings less distinctly infumate.....7

7. Face of female densely punctate; metapleurum rather sparsely punctate; fore tibia of female strongly swollen at middle (fig. 2); middle tibia black basad of white annulus. (male not distinguishable from *P. aequalis* with certainty) **inflata**

Face of female sparsely punctate; metapleurum densely punctate and more or less striolate; fore tibia of female moderately swollen at middle (fig. 3); middle tibia basad of white annulus dusky ferruginous.....**aequalis**

Pimpla sodalis Ruthe

Pimpla sodalis Ruthe, Stettin. Ent. Zeit. 1859. 20: 371. ♂ ♀
Pimpla nordenskioldi Holmgren, Oefvers. Svensk. Vet-Akad. Forh. 1879. 29: 97. ♀
Pimpla longiceps Thomson, Opusc. Ent. 1877. 8: 1877. ♂ ♀
Ephialtes (*Ephialtes*) *sodalis* Cushman, Proc. U. S..Nat. Mus. 1920. 58: 332.
Pimplidea sodalis Roman, Troms. Museum Arshefter. 1931. v. 54, no. 4, p. 12.

There are additional references in European literature dealing with the synonymy and distribution of this species.

Female.—No females are available for study. They are colored like the males.

Male.—Wing 4–5 mm. Black, the legs ferruginous as follows: front and middle legs beyond the trochanters, hind femur, and the base of the hind tibia. The front and middle femora are blackish at their bases and the red on the hind tibia passes into black at about the middle.

Epipleura similar to those of *P. tenuicornis* (fig. 5).

Material: ♂, Nazan Bay, Atka, Aleutian Islands, VII–28–07, E. C. VanDyke (Cornell); ♂, Churchill, Ont., VII–3–34, A. M. Heydweiller (Townes). The species is known also from Greenland, Iceland, and the alpine levels of the mountains of Norway, Scotland, the Pyrenes, and the Swiss Alps.

Pimpla maura Cresson

Pimpla maura Cresson, Trans. Amer. Ent. Soc. 1870. 3: 143. ♀
Pimpla maura Riley and Howard, Bull. U. S. Dept. Ent. n. ser. 1902. 38: 109.
Pimpla maura Morley, Rev. Ichn. Brit. Mus. 1914. 3: 65.
Ephialtes (*Ephialtes*) *maura* Cushman, Proc. U. S. Nat. Mus. 1920. 58: 331.
Ephialtes maura Brimley, Ins. of N. C. 1938. p. 409.

Female.—Wing 8–12 mm. Black, white as follows: sometimes the front part of the tegula, a spot on the scutellum, more or less of fore femur and tibia in front, tip of middle femur in front, and sometimes a

small obscure spot near the lateral apical corners of tergites 3–6. Wings fuscous.

Face short, densely punctate; front tibia weakly swollen at its middle (fig. 1); pleura mat and densely punctate, the metapleurum very obscurely striolate; propodeum densely punctate and finely rugose above, more strongly rugulose toward the mid-line; basal carinae of the propodeum obsolete; third abdominal tergite subpolished, rather densely punctate except along the apical margin; epipleura of segments 2 to 4 nearly 4.0 as long as wide.

Male.—Black, white as follows: scape in front, tegula, scutellum, postnotum, front and middle tarsi except the tips of the segments, spot on front coxa and usually one on middle coxa, front femur and at least the tip of the middle femur in front, front and middle tibiae except for a line behind, and an incomplete subbasal annulus on the hind tibia. Wings lightly fuscous. Otherwise similar to the female except for the usual sexual differences.

Material: ♀, Waccamaw Lake, N. C., IV–?–20 (U. S.); ♂, Brookfield, Fla., IV–20–18, *ex Hemerocampa leucostigma* (U. S.); ♀, La. Belle, Fla., IV–?–21, J. N. Knull (U. S.); ♀, Paradise Key, Fla., IV–1–19, C. A. Mosier (U. S.); ♀, Victoria, Tex., VI–1–15, J. D. Mitchell (U. S.); ♂, Tex., Coll. Belfrage (U. S.). Riley and Howard record this species from French Creek, W. Va., where it was reared from pupae of *Malacosoma americana* by F. E. Brooks. Morley records the species from Georgia, and Brimley records the North Carolina specimen listed above from Waccamaw Lake.

Pimpla pedalis Cresson

Pimpla pedalis Cresson, Proc. Ent. Soc. Phila. 1865. 4: 268. ♂
Pimpla pedalis Walsh, Trans. Acad. Sc. St. Louis. 1873. 3: 132.
Pimpla pedalis Provancher, Nat. Canad. 1880. 12: 35.
Pimpla pedalis Provancher, Faune ent. Canada. Hymen. 1883. p. 456.
Pimpla pedalis Fernald, *in* Forbush and Fernald: The Gypsy Moth. 1896. p. 377.
Pimpla pedalis Fiske, N. H. Agric. Exp. Sta. Tech. Bull. 1903. 6: 201–202.
Pimpla pedalis Howard and Fiske, U. S. Dept. Agric. Bur. Ent. Bull. 1911. 91: 137–138, 144, 147–149, 237–239.
Pimplidea pedalis Viereck, Bull. U. S. Nat.,Mus. 1914. 83: 117.
Pimpla pedalis Morley, Rev. Ichn. Brit. Mus. 1914. 3: 63.
Scambus (*Pimplidea*) *pedalis* Viereck, Hym. Conn. 1916. p. 320.
Ephialtes (*Ephialtes*) *pedalis* Cushman, Proc. U. S. Nat. Mus. 1920. 58: 333.
Ephialtes pedalis Schaffner and Griswold, Misc. Pub. U. S. Dept. Agric. 1934. 188: 142.

Only the more important references are included above.

Female.—Wing 8–13 mm. Black with legs ferruginous except as follows: hind leg with tibia, tarsus, and tip of femur black; front coxa all or mostly black; apical segments of palpi somewhat brownish; wings hyaline.

Face rather sparsely punctate; front tibia weakly swollen at the middle (fig. 1); pleura moderately punctate, the metapleurum usually rather strongly striolate; propodeum punctate and irregularly striolate

above, its basal carinae subobsolete; third abdominal tergite subpolished, rather densely punctate except along the apical margin; epipleura of segments 2–4 about 3.5 as long as wide.

Male.—Scape often with a white spot in front. Otherwise similar to the female except for the usual sexual differences.

This species should perhaps be considered a subspecies of the European *Pimpla arctica* Zett., which differs from *pedalis* mainly in having the middle coxa black. *Pedalis* is the only Nearctic species with the hind tibia entirely black. It is exceptional for the tribe in that the male averages almost as large as the female.

Material: 150 ♂, 102 ♀, from N. S. (Truro), P. Q. (Boucherville, Joliette, Laval Co., and Montreal), Ont. (Salines and Waubamic), Vt. (Rutland and Woodstock), Mass. (Princeton and So. Hadley), R. I. (Westerly), N. Y. (Allegheny State Park, Bemus Point, Blue Mt., Canadarago Lake, Chafee, Downsville, East Greenbush, Farmingdale, Geneva, Hancock, Hilton, Honeoye Falls, Horton, Ithaca, Jamesville, Little Genesee, Lockport, Manlius, McLean, Milford Center, New Berlin, New Russia, Niagara Falls, Oak Orchard Swamp, Olcott, Oneonta, Oswego, Otsego Lake, Otto, Patterson, Portageville, Potsdam, Poughkeepsie, Randolph, Rhinebeck, Riverhead, Rome, Slaterville, Slide Mt. at 4,000 ft., Springlake, Syracuse, Troy, Whitesville, and Yonkers), N. J. (Moorestown), Ohio (Akron and Put-in-Bay), Mich. (Alcona Co., Cheboygan Co., Clare Co., Iosca Co., Keweenaw Co., Midland Co., Missaukee Co., and Osclola Co.), Sask. (Waskesiu), Alta. (Shovel Pass in Jasper Park), B. C. (Robeson), Calif. (Sonoma Co.), Ariz. (Mt. Lemon in Santa Catalina Mts.), and N. Mex. (Jemez Springs at 6,400 ft.). The species has been recorded from the additional localities of Me. (Hamden and Orono), Vt. (White Face), N. H. (Tamworth and Conway), Conn. (Lymne, Mansfield, Meriden, New Haven, and Portland), Mass. (Arlington, Gardner, and Melrose), N. Y. (Fisher's Island, Flatbush, Glens Falls, Melville, New Baltimore, and Utica), Pa., Md., Va., Ill., Ut., Ore., and Man. The type is from Colorado. In the vicinity of Ithaca, N. Y., it has been collected from May 10 to October 16.

This is an abundant species in the Canadian Zone and is common in the Transitional. It is a species of mesophytic woodlands. It is listed in literature as a parasite of Tortricidae, (*Archips argyrospila*, and *A. fumiferana*) Lasiocampidae (*Malacosoma americana* and *M. disstria*), Lymantriidae (*Euproctis*

phaeorrhoea, *Lymantria dispar*, *Notolophus antiqua badia*, and *Olene plagiata pinicola*), Notodontidae (*Heterocampa guttivitta* and *H. leucostigma*), Noctuidae (*Cirphis unipuncta*) and Arctiidae (*Halisidota caryae* and *Isia isabella*), and has been reared from galls of *Saperda concolor* (Cerambycidae) on willow. It has been recorded as overwintering in pupae of *Heterocampa guttivitta* and as having been bred from the pupae of *Archips fumiferana* the larvae of which had been received by mail and kept where they could not be parasitized by adults. It has once been recorded as ovipositing in the larvae of *Malacosoma disstria*. According to Schaffner and Griswold there are two or more generations a year in the Northeast and it overwinters in the host pupa.

Pimpla aquilonia Cresson

Pimpla turionellae authors (in part, not Linnaeus).
Pimpla aquilonia Cresson, Trans. Amer. Ent. Soc. 1870. 3: 145. ♂
Pimpla flavicoxis Thomson, Opusc. Ent. 1877. 8: 747. ♂ ♀
? *Meniscus marginatus* Provancher, Nat. Canad. 1883. 14: 15. ♀
Bassus cylindricus Provancher, Addit. Faune Ent. Can. Hymen. 1889. p. 111. ♂
Pimpla inquisitor Davis, Proc. Acad. Nat. Sci. Phila. 1894. p. 190.
Pimpla annulipes Davis, Trans. Amer. Ent. Soc. 1895. 22: 30.
Pimplidea tenuicornis Cushman, Proc. Ent. Soc. Wash. 1918. 20: 9–10. (in part).
Iseropus coelebs Cushman, Proc. Ent. Soc. Wash. 1918. 20: 12 (in part).
Ephialtes (*Ephialtes*) *aquilonia* Cushman, Proc. U. S. Nat. Mus. 1920. 58: 337.
Ephialtes (*Ephialtes*) *aquilonia*, Cushman *in* Leonard: List Ins. of N. Y. 1928. p. 936.

There are other references to this species in European literature. In America the females have been confused with *P. tenuicornis* and the majority of males (those with a black scutellum) with *P. aequalis*. The majority of Palaearctic references to *P. turionellae* (of authors, not Linnaeus, =*contemplator* Mueller) refer to *aquilonia* as it is the commonest of its general appearance in Europe. However, one or more others closely resembling the present species occur in Europe, and the majority of European authors make no effort to distinguish between them.

I have corresponded with Mr. J. F. Perkins of the British Museum regarding the names *flavicoxis* Thomson and *contemplator* Mueller. Mr. Perkins has given the European species of *Pimpla* a special study and has seen the type of *flavicoxis* Thomson. He is of the opinion that *flavicoxis* is a synonym of *aquilonia*. Regarding *contemplator*, he writes as follows: "*Pimpla contemplator* is a species quite distinct from *P. flavicoxis*. The type of *contemplator* as far as is known, is destroyed, and the first reviser of this species is Gravenhorst. I have seen the series in Gravenhorst's collection, and this agrees with Thom-

son's interpretation of *turionellae L.*, which of course is not the true *turionellae* of Linnaeus (=*examinator* Fab.). The epipleura of *flavicoxis* are very narrow, whereas those of *contemplator* are broader, with those of the fourth segment almost as broad as long." *Contemplator* is rather similar to the Nearctic *aequalis*.

I have examined the type of *Meniscus marginatus* Provancher and found that it probably belongs to this species, though the poor condition of the type and certain abnormalities of coloration prevented me from being certain of it.

Female.—Wing 4–9 mm. Black, the flagellum beneath and the palpi toward the end reddish brown. Legs ferruginous, front coxa blackish at base and hind tibia and tarsus black with an annulus covering the second fourth of the tibia and the tibial spurs white; base of tarsal segments brownish. Wings hyaline.

Face moderately punctate; front tibia moderately swollen at middle; pleura rather densely and finely punctate, the meso- and metapleura near their coxae slightly striate; propodeum moderately punctate and irregularly transversely striolate above; third abdominal tergite mat and moderately punctate; epipleurum of second segment about 5.0 as long as wide, that of the fourth segment about 2.4 as long as wide (fig. 4).

Male.—Scape in front, palpi, tegula, and often the scutellum white; front coxa not marked with blackish. Otherwise similar to the female except for the usual sexual differences. The male may easily be recognized by the white on the scape in front, this character being shared only with *P. pedalis*. Occasional very small males have the scape entirely black. The scutellum is marked with white in about 30 per cent of the specimens.

Material: 81 ♂, 65 ♀, from N. S. (Millsville), N. B. (St. John and Nerepis), P. Q. (Sherbrooke and Stoneham), Ont. (Biscotasing, Perry Sound, and Waubamic), Me. (Bar Harbor and Hartland), N. H. (Mt. Madison and Pinkham Notch), Mass. (Fitchburg and South Hadley), Conn. (Candlewood Lake), N. Y. (Allegheny State Park, Herkimer, Ithaca, Laborador Lake, McLean, North Fairhaven, Oneonta, Poughkeepsie, Rock City, Shokan, and Slide Mt. at 2,800–4,000 ft.), Minn. (Itaska Park), Sask. (Waskesiu), and Alaska (Reindeer Camp at Golovin, Savonoski, and Seward). The type of *aquilonia* is from Maine, that of *marginatus* from Quebec, and that of *cylindricus* from Cap Rouge, P. Q. The specimens from Bar Harbor, Me., were reared from *Coleophora salmani* by R. L. Taylor. At Ithaca, N. Y., this species has been collected from May 8 to September 25. In the Palaearctic Region the species is apparently widespread and abundant. I have seen specimens from Sweden, Germany, and Japan.

This species is abundant in the Canadian Zone and occurs in some numbers in the Transitional, but here rather restricted to localities with a more northern fauna. It prefers woods with a rank undergrowth of herbage.

Pimpla tenuicornis Cresson

Pimpla tenuicornis Cresson, Proc. Ent. Soc. Phila. 1865. 4: 267. ♀
Pimpla tenuicornis Provancher, Nat. Canad. 1880. 12: 35.
Pimpla tenuicornis Provancher, Faune ent. Canada Hymen. 1883. p. 457.
Pimpla turionellae Morley, Rev. Ichn. Brit. Mus. 1914. 3: 66 (in part, not Linnaeus).
Scambus (*Delomerista*) *tenuicornis* Viereck, Hym. Conn. 1816. p. 322.
Scambus (*Pimplidea*) *turionellae* Bradley, Bull. Brooklyn Ent. Soc. 1918. 13: 104 (in part, not Linnaeus).
Pimplidea tenuicornis Cushman, Proc. Ent. Soc. Wash. 1918. 20: 9–10 (in part).
Ephialtes (*Ephialtes*) *tenuicornis* Cushman, Proc. U. S. Nat. Mus. 1920. 58: 338 (in part).

There are a few additional records in literature regarding hosts and distribution, but as they are possibly based upon misdeterminations and are of no great importance, they are omitted.

Female.—Wing 4–8 mm. Black, basal part of flagellum and apical segments of palpi dusky red; legs red as follows: front and middle legs except that the front coxa is mostly black, and hind coxa, trochanters, and femur except its tip; hind tibia with a narrow dirty white annulus about as long as the third hind tarsal segment; hind tarsi blackish brown. Wing slightly infumate.

Face long, sparsely and weakly punctate; front tibia somewhat swollen at the middle; mesopleurum rather sparsely and weakly punctate; metapleurum rather densely and weakly punctate and somewhat striolate; propodeum rather sparsely and weakly punctate above; third abdominal tergite polished and rather densely punctate except along the apical margin; epipleurum of second segment about 5.0 as long as wide, that of the fourth segment about 1.7 as long as wide (fig. 5).

Male.—Similar to the female except for the usual sexual differences.

Material: 106 ♂, 40 ♀, from N. S. (Truro), N. B. (Nerepis and St. John), P. Q. (Louisville, Montreal, Sherbrooke, St. Anne's, and Stoneham), Ont. (Salines and Waubamic), Sask. (Waskesiu), N. H. (Mt. Madison), Vt. (Rutland and Woodstock), Mass. (South Hadley), R. I. (Westerly), N. Y. (Barnum Point, Bemus Point, Caroline, Downsville, Geneva, Greene Co. at 2,500 ft., Hancock, Horton, Ithaca, Lockport, McLean Bogs, New Berlin, North Blenheim, Olean, Oneonta, Oswego, Otsego Lake, Penn Yan, Potsdam, Poughkeepsie, Rome, Saranac Lake, Seneca Junction, Shokan, Spring Lake, Stony Island, and Utica), Mich. (Agricultural College, Alcona Co., Iosco Co., Isabella Co., and Midland Co.), and Colo. It has been collected from May 8 at Ithaca, N. Y., to September 25 at Geneva,

N. Y. The type of *tenuicornis* is from Colorado. Cushman records the species (correctly ?) from the additional localities of Vancouver, N. J., and Ill. It has been recorded (correctly ?) as a parasite of *Lymantria dispar* and *Sesia caudata*.

This species is common in the Canadian Zone and occurs in moderate numbers in the Transitional. I have not seen specimens from the Upper Austral Zone.

Pimpla nuda n. sp.

Pimpla tenuicornis authors (in part).

Female.—Wing 4–7.5 mm. Black with red legs except as follows: flagellum brown, paler toward the base; apical three segments of palpi brownish; base of front coxa black; basal fourth of middle tibia blackish; hind tibia black except for a white annulus occupying a sixth to a fifth of its length; hind tarsus and tip of hind femur black; wings very slightly infumate.

Face sparsely punctate; front tibia slightly swollen at the middle (fig. 3); pleura sparsely and weakly punctate, the metapleura near the coxa finely and weakly striate; propodeum irregularly punctate above; hind tibia with the hairs on its outer edge sparse, in some places their bases separated from each other by more than the length of the hairs, the rest of the tibia with the hairs of normal density (this is the only species of *Pimpla* known to me with the hair sparser on the outer edge of the hind tibia); third abdominal tergite subpolished, rather densely punctate except along the apical margin; epipleurum of second segment about 1.7 as long as wide, that of the fourth segment about 1.3 as long as wide.

Male.—Unknown. It may be that the male of this species has the tegula white and the hind tibia uniformly hairy, in which case it is confused with the male of *P. aequalis*.

Type: ♀, Camp Roosevelt, Lake Sebago, Bear Mt. State Park, N. Y., VIII–8–36, H. Townes (Townes). Paratypes: 3 ♀, Ithaca, N. Y., VII–9–04, VIII–9–25, and VI–9–35, P. P. Babiy *et al.* (Cornell); ♀, McLean, N. Y., VIII–8–21 (Cornell); ♀, Milford Center, N. Y., VII–13–35, H. Townes (Townes); ♀, Troy, N. Y., H. Townes (Townes); ♀, Bay Co., Mich., VI–19 32, R. R. Dreisbach (Dreisbach); ♀, Iosco Co., Mich., VII–16 to 17–38, R. R. Dreisbach (Dreisbach); ♀, Midland Co., Mich., IX–12–38 R. R. Dreisbach (Townes); ♀, Mooresville, Pa., VII–13–17, J. Primm (U. S.); ♀, IV–28–16, F. A. Fenton, bred from lepidopterous pupa (U. S.).

Pimpla inflata n. sp.

Pimpla annulipes Riley, Ann. Rep. Ins. Mo. 1873. 5: 49 (misidentification of *annulipes* Brulle).

Pimpla aequalis authors (in part).

In the U. S. National Museum are specimens from the Riley collection reared from codlin moth and they are very likely the same specimens referred to in the above note by Riley. Probably most North American records of *Pimpla* bred from the codlin moth apply to the present species.

Female.—Wing 5–7.5 mm. Black with red legs except as follows: apical segments of palpi brownish; tegula white; more or less of front coxa blackish; middle tibia with a white annulus, blackish basad of the annulus and dusky on the outer side between the annulus and the tip; hind tibia black with a white annulus; apex of hind femur black; hind tarsi dark brown, paler toward the bases of the segments. Wings hyaline.

Face rather densely punctate; front tibia very strongly inflated at the middle (fig. 2); pleura rather weakly punctate; propodeum moderately and evenly punctate above; third abdominal tergite subpolished, rather densely punctate; epipleurum of second segment about 2.0 as long as wide, that of the fourth segment about 1.3 as long as wide.

Male.—I have seen males of this species reared with females from *Laspeyresia molesta*. Except that the middle tibia averages darker, they do not differ from males of *P. aequalis* and are doubtless confused with this species. I have compared the genitalia of the two and find that the tip of the penis appears to be slightly narrower in *P. inflata* than in *P. aequalis*, but there is not enough difference here to aid materially in determinations.

Type: ♀, Camp Roosevelt, Lake Sebago, Bear Mt. State Park, N. Y., VII–8–36, H. Townes (Townes). Paratypes: ♀, Montreal, Que., "VI–22" (Cornell); ♀, Bemus Point, N. Y., VIII–14–37, H. Townes (Townes); 5 ♀, Ithaca, N. Y., June 8 to Aug. 4, P. P. Babiy *et al.* (Cornell); ♀, Minetto, N. Y., VIII–4–38, W. D. Wylie (Townes); ♀, Shokan, N. Y., VII–11–36, H. Townes (Townes); ♀, Mass., C. F. Baker (U. S.); 5 ♀, Arendtsville, Pa., VI–21–21, S. W. Frost (Cornell); ♀, Harrisburg, Pa., V–31–08, P. R. Myers (U. S.); ♀, Siloam Springs, Ark., VI–5–08, S. W. Frost *ex Laspeyresia pomonella* (U. S.); ♀, Ind., (U. S.); ♀, Algonquin, Ill., C. F. Baker (U. S.); 2 ♀, Monticello, Fla., adults emerged IV–38–13 and V–2–13 from material collected IV–18–33 by J. B. Gill, host *Proteropteryx bolliana*, specimen had been determined as "*Itoplectis marginatus* Prov." (U. S.); ♀, Tex., Coll. Belfrage, labeled "*Colpomeria americana* Ash." (U. S.); 11 ♀, C. V. Riley Collection, *ex Laspeyresia pomonella* (U. S.); ♀, Quaintance No. 7464, *ex Laspeyresia pomonella* (U. S.). Also, I have seen a series of males and females at the Moorestown, N. J. experiment station that were reared from *Laspeyresia molesta* by "Oriental Fruit Moth Investigations."

Pimpla aequalis Provancher

Pimpla annulipes authors (in part, not Brulle).
Pimpla aequalis Provancher, Nat. Canad. 1880. 12: 36. ♀
Pimpla aequalis Provancher, Faune ent. Canada Hymen. 1883. p. 457.
Meniscus ashmeadii Provancher, Addit. Faune Canada Hymen. 1889. p. 430. ♀
Pimpla conquisitor var. *rufuscula* Davis, Trans. Amer. Ent. Soc. 1897. 24: 368. ♀
Pimpla turionellae Roman, Ent. Tidskrift. 1910. 31: 187 (in part, not Linnaeus).
Pimpla turionellae Morley, Rev. Ichn. Brit. Mus. 1914. 3: 66 (in part, not Linnaeus).
Itoplectis rufuscula Watson, J. Econ. Ent. 1916. 9: 527.
Scambus (*Itoplectis*) *marginatus* Viereck, Hymen, Conn. 1916. p. 322 (in part, not Provancher).
Scambus (*Pimplidea*) *turionellae* Bradley, Bull. Brooklyn Ent. Soc. 1918. 13: 104 (in part, not Linnaeus).
Pimplidea aequalis Cushman, Proc. Ent. Soc. Wash. 1918. 20: 9–10.
Ephialtes (*Ephialtes*) *aequalis* Cushman, Proc. U. S. Nat. Mus. 1920. 58: 338 (in part).

There are many references to *Pimpla annulipes* and *P. aequalis* in literature. The majority refer to the present species, but since a large number of them are doubtless based upon misdeterminations of other species it seems unnecessary to include them above.

Female.—Wing 3–10 mm. Black with ferruginous legs except as follows: flagellum brownish, paler toward the base; maxillary palpus mostly yellowish or pale brown; tegula whitish, usually with more or less of the apex brownish; middle tibia dusky red with a whitish subcomplete annulus; hind tibia black with a white annulus; hind tarsus brown with the apex of the segments darker; sometimes the underside of abdominal segments 2–4 fulvous and the latero-apical corners and apical margins of the tergites more or less rufous. Wings hyaline.

Face sparsely punctate; front tibia moderately swollen at the middle; pleura rather densely punctate, the metapleura and lower part of mesopleura often striate; propodeum densely and evenly punctate above, its basal carinae moderately strong; third abdominal tergite subpolished, rather densely punctate except along the apical margin; epipleurum of second segment about 1.6 as long as wide, that of the 4th segment about 1.3 as long as wide (fig. 6).

Male.—Tegula white; middle tibia red with a white annulus; underside of segments 2–4 rarely fulvous, the tergites uniformly black. Otherwise, except for the usual sexual differences, similar to the female.

The variety with the rufous markings on the abdomen of the female is commoner in the southern part of the range of the species and averages slightly larger than the dark variety. The types of *aequalis*, *ashmeadii*, and *rufuscula* all belong to the former variety.

Material: 661 ♂, 366 ♀, from Me. (Mt. Desert), N. H. (Hanover), Mass. (So. Hadley), Conn. (Canterbury, Milford, and Stonington), R. I. (Alton, Ashaway, Charlestown, and

Westerly), N. Y. (Armonk, Babylon, Bear Mt. State Park, Bemus Point, Canadarago Lake, Canajoharie, Caroline, Downsville, Farmingdale, Ithaca, Jamesville, McLean, Milford Center, Millwood, North Fairhaven, Oneonta, Penn Yan, Poughkeepsie, Rochester Junction, Rock City, Shokan, Slide Mt. 2,800–4,000 ft., Syracuse, and Utica), Pa. (Arendtsville, Carlisle Junction, Fairview, Highspire, Hillsgrove, Inglenook, Linglestown, North East, and Paupack), N. J. (Riverton), Md. (Cabin John, Glen Echo, Plummer's Island, Reistertown, and Ringgold), Va. (Falls Church, Great Falls, Norfolk, and Warm Springs Mt. 3,300 ft.), W. Va. (Kanawha Station and Terra Alta), N. C. (Murfreesboro, Raleigh, and Wendall), S. C. (Greenville), Tenn. (Clarksville), Ala. (Coleta, Longdale, and Pyziton), Fla. (Bradenton, Dunedin, and Ocala), La., Tex. (Dallas), Ohio (Adams Co., Columbus, and Sandusky), Ind., Ill. (Algonquin and Urbana), Mich. (Agricultural College, Alcona Co., East Lansing, Genesee Co., Iosca Co., Lapeer, Midland Co., Ontanagon Co., Osclola Co., and Wayne Co.), Ark. (Bentonville), Ia. (Muscatine), and Neb. At Ithaca, N. Y., collection dates are from May 1 to Oct. 16. Cushman records the species from the additional localities of N. B., Ga., Wis., Mo., Colo., and N. Mex. The type of *aequalis* is probably from Quebec, that of *ashmeadii* is from Jacksonville, Fla., and that of *rufuscula* from northern Illinois.

Since a few of the males that I have determined as this species probably belong to *P. inflata*, I have included in the above list of localities only those from which I have female specimens. I have before me, also, male specimens doubtless of this species from Ontario, Quebec, and New Brunswick.

This species is the most abundant of its genus in the Transitional Zone and records indicate that it is also common in the Upper and Lower Austral Zones. In the Canadian Zone it is largely replaced by *aquilonia*. It occurs in the undergrowth of woods and apparently is to be found all over the United States east of the Rocky Mountains. About 85% of the females of this species belong to the variety without rufous markings on the abdomen. Males rarely have the underside of the abdomen largely rufous, but never the apical margins of the tergites rufous.

Among the material before me is a female bred from *Laspeyresia molesta* by H. S. McConnell at Ringgold, Md., a female bred from *Laspeyresia pomonella* by Moulton in Nebraska, and

a male and two females bred from *Coleophora salmani* at Mt. Desert, Me.

Genus **Apechthis** Foerster

Ephialtes Schrank, Fauna Bioca. 1802. vol. 2, pt. 3, p. 316 (not *Ephialtes* Gravenhorst 1829 and later authors). Genotype: *Ichneumon compunctor* Linnaeus.
Apechthis Foerster, Verh. naturh. Ver. preuss. Rheinland. 1868. 25: 164. Genotype: *Ichneumon rufatus* Gmelin.
Apechtis Thomson, Opusc. Ent. 1889. fas. 13, p. 1,410. Genotype: *Pimpla flavonotata* Homgren (= *Apechthis rufatus* Gmelin).

This genus is easily distinguished from the others discussed in this paper by the hook at the end of the ovipositor and the whitish face of the male. Besides the following three, two other species (*componotus* Davis and *pacificus* Cushman) occur in the Nearctic Region, both in the northwestern part of the United States. These are both unknown to me.

My reasons for using the name *Apechthis* rather than *Ephialtes* are discussed under the genus *Pimpla*.

KEY TO SPECIES OF APECHTHIS OF EASTERN NORTH AMERICA

1. Petiole convex above, but not pyramidally elevated near the middle; hind tarsal claws of female without a tooth, in this way differing from the claws of the fore and middle tarsi ..... **ontario**
   Petiole pyramidally elevated near the middle; hind tarsal claws of female with a tooth as in the claws of the fore and middle tarsi 2
2. Males 3
   Females 4
3. Basal two segments of hind tarsus white with their apices blackish; face entirely white ..... **annulicornis**
   Basal two segments of hind tarsus black or brown with their apices black; face usually with a central stripe and a triangle under each antenna black, the rest yellowish white ..... **picticornis**
4. Tegula white; basal two segments of hind tarsus white with their apices blackish; hind tibia with a white annulus covering slightly less than the middle half ..... **annulicornis**
   Tegula mostly brown; basal two segments of hind tarsus brown with their apices darker; hind tibia with a yellowish white annulus above the middle covering slightly less than a third of its length ..... **picticornis**

Apechthis ontario Cresson

Pimpla ontario Cresson, Trans. Amer. Ent. Soc. 1870. 3: 146. ♂
Pimpla ontario Provancher, Nat. Canad. 1880. 12: 37. ♂ ♀
Pimpla ontario Provancher, Faune ent. Canada. Hymen. 1883. p. 458.
Pimpla ontario Johannsen, Maine Agr. Exp. Sta. Bull. 1913. 210: 26.
Apechtis ontario Morley, Rev. Ich. Brit. Mus. 1914. 3: 33.
Apechthis ontario Cushman, Proc. U. S. Nat. Mus. 1920. 58: 354.
Apechthis ontario Proctor, Biol. Surv. Mt. Desert Region. 1938. 6: 406.

Female.—Wing 6.5–11 mm. Black. Anterior orbit below antenna, at the summit, and sometimes above the antenna narrowly yellowish white; front of pedicel and flagellum whitish, the flagellum grading to dusky orange toward the tip; clypeus orange to black; mandible usually with a paler spot; maxillary palpus orange; labial palpus dusky orange; tegula white to entirely brown; humeral angle of pronotum, tip of

scutellum, and metanotum white. Legs ferruginous except as follows: front coxa blackish at base; middle tibia with an indistinct white annulus, more or less dusky basad of the annulus and sometimes dusky beyond it; front and middle legs somewhat varied with whitish; tip of hind femur dusky; hind tibia black (or sometimes dusky red) with a white annulus occupying from one fourth to nearly half its length; hind tarsi blackish with the first segment except its apex and usually the base of the second segment whitish.

Hind tarsal claws without a large basal tooth, in this way differing from the claws of the front and middle tarsi; upper surface of petiole rather weakly elevated at about two thirds its length.

Male.—Colored like the female except that the face, anterior orbits, clypeus, mandible except tip, palpi, scape beneath, and tegula are white. The legs have slightly more extensive white markings and the tarsal claws are simple.

This species is very distinct from the other Nearctic species in having the petiole less strongly elevated and lacking the tooth on the hind tarsal claws of the female. In these respects it agrees with the European *resinator* Thunberg and perhaps should be considered the same species. According to the specimens before me, *resinator* differs constantly in having the petiole more strongly elevated at the middle and the leg markings dusky red instead of black or a darker dusky red.

Material: ♂, Truro, N. S., VII–15–13, R. Matheson (Cornell); ♀, Truro, N. S., VIII–12–13, R. Matheson (Cornell); ♀, St. Godefroi, P. Q., VII–2–35, H. B. Hoeffler (Townes); ♂, Slide Mt. (2,000–4,000 ft.), N. Y., VIII–25–35, H. and C. Townes (Townes); ♀, Oneonta (swamp at 1,900 ft.), N. Y., VIII–18–35, H. Townes (Townes); ♀, Kodiak, Alaska, IX–13–19, J. S. Hine (Univ. Ohio); ♀, Robeson, B. C., X–6–38, H. R. Foxlee (Townes); 2 ♀, Ingleside, Calif., VIII–2–08, J. C. Bradley (Cornell); 3 ♀, Leona Hgts., Calif., VIII–27–08, J. C. Bradley (Cornell); 3 ♀, Mesa Grande, Sonoma Co., Calif., VII–?–08, J. C. Bradley (Cornell); 46 ♀, Muir Woods, Calif., VIII–30–08, J. C. Bradley (Cornell); ♀, Sisson, Calif., VIII–14–08, J. C. Bradley (Cornell). Cresson's type is from Canada, probably Ontario. Mr. Cushman tells me that there are specimens at the National Museum from N. S., Que., Ont., N. Y., Mich., Ida., Wash., Vancouver, and Calif. Most of the Canadian specimens were reared from *Archips fumiferana*. A female from Sonoma Co., Calif., was caught while ovipositing in a *Tortrix* on wild pea. Morley records this species from Nova Scotia, Proctor records it from Bar Harbor, Me., Jul. 7 to Aug. 10, and Johannsen bred specimens from *Archips fumiferana* at Greenville Junction and Houlton, Maine.

In the East this is a species of the Canadian Life Zone and is rare in warmer localities.

Apechthis annulicornis Cresson

Pimpla annulicornis Cresson, Trans. Amer. Ent. Soc. 1870. 3: 147. ♂ ♀
Pimpla annulicornis Walsh, Trans. Acad. Sc. St. Louis. 1873. vol. 3, pt. 1, p. 135.
Pimpla annulicornis Provancher, Nat. Canada. 1880. 12: 37.
Pimpla annulicornis Provancher, Faune ent. Canada. Hymen. 1883. p. 458.
Scambus (*Pimplidea* ?) *annulicornis* Viereck, Hym. Conn. 1916. p. 321.
Scambus (*Apechtis*) *annulicornis* Bradley, Bull. Brooklyn Ent. So. 1918. 13: 104.
Apechthis picticornis Cushman, Proc. U. S. Nat. Mus. 1920. 58: 352 (in part, not Cresson).
Apechthis picticornis Cushman, *in* Leonard: List Ins. of N. Y. 1928. p. 937 (not Cresson).
? *Apechthis picticornis* Schaffner and Griswold, U. S. Dept. Agr. Misc. Pub. 1934. 188: 99, 142.

In 1920 Cushman synonymized this species with *picticornis* and since that time it has been included under *picticornis* in literature.

Female.—Wing 8–12 mm. Black. Most of the anterior orbit in front and often a small spot at the top of orbit, white; front of scape and pedicel white; flagellum in front yellowish white grading to orange at the apex; spot on mandible whitish; apical three or four segments of maxillary palpi and apical segment of labial palpus pale; tegula, humeral angle of pronotum, top of scutellum, and metanotum white. Legs ferruginous somewhat varied with whitish except as follows: basal two thirds of front coxa blackish; tip of hind femur dusky; hind tibia black with a white band occupying slightly less than its middle half; hind tarsi whitish except that the apex of the first three segments and all except seometimes the extreme base of the last two segments are blackish.

All tarsal claws with a prominent basal tooth; peticle subpyramidally elevated just behind the middle.

Male.—Colored like the female except that the face, clypeus, and palpi are entirely white; the upper margin of the mesopleurum beneath the tegula is white; most of the front coxa and somewhat more extensive markings on the front and middle legs are white; and the white band on the hind tibia occupies slightly more than the middle half of its length. The tarsal claws are simple.

Material: 32 ♂, 37 ♀, from Mass. (South Hadley), Conn. (Ledyard and Stonington), R. I. (Westerly), N. Y. (Bemus Point, Farmingdale, Hancock, Ithaca, Millwood, New Berlin, North Petersburg, and Poughkeepsie), Mich. (Midland Co.), Pa. (Paupack), N. J. (Moorestown), and Md. (Reistertown). Collection dates range from May 9 at Ithaca, N. Y., to Sept. 10 at Westerly, R. I. Cresson described the species from Pa. and Ill. Cushman records it from Texas. Schaffner and Griswold reared two specimens of "*Apechthis picticornis*" from 2,956

larvae of *Ennomos subsignarius* collected in Mass. Judging from the locality, they probably had this species rather than the true *picticornis*. I have examined the specimens of "*picticornis*" recorded by Cushman from N. Y. and find them all to be *annulicornis*.

This is the commonest species of its genus in the Transitional Zone and in the eastern United States the only one that appears in areas warmer than the Transitional. I found it common at Farmingdale on Long Island, N. Y.

Apechthis picticornis Cresson

Pimpla picticornis Cresson, Trans. Amer. Ent. Soc. 1870. 3: 146. ♂
Pimpla picticornis Provancher, Nat. Canad. 1880. 12: 38.
Pimpla picticornis Provancher, Faune ent. Canada. Hymen. 1883. p. 459.
Apechtis annulicornis Morley, Rev. Ichn. Brit. Mus. 1914. 3: 33 (not Cresson).
Scambus (*Tromatobia* ?) *picticornis* Viereck, Hym. Conn. 1916. p. 322.
Apechthis picticornis Cushman, Proc. U. S. Nat. Mus. 1920. 58: 352 (in part).
Apechthis ornatulus Walley, Can. Ent. 1929. 41: 190. ♂, n. syn.

Female.—Wing 9–13 mm. Black. Small orbital mark just below the antenna pale yellow; front of scape more or less reddish; flagellum in front yellowish white grading to orange at the tip; spot near base of mandible pale yellow; apical one or two segments of maxillary palpus somewhat orange; tegula fuscous, partly yellowish; tip of scutellum and metanotum white; most of front coxa and a small spot at the tip of hind femur black, the rest of the legs ferruginous varied with whitish except for the hind tibia and tarsus. Apical half and slightly less than the basal fourth of hind tibia, tips of first three segments and the apical two segments of hind tarsus entirely black; the rest of the hind tibia and tarsus brownish yellow.

All tarsal claws with a prominent basal tooth; petiole subpyramidally elevated just behind the middle. The abdomen is very slightly less coarsely and distinctly punctate than in *annulicornis*.

Male.—Colored like the female except as follows: hind tarsus except the base of the first or the first and second segments entirely black; face except usually a central stripe and a triangle below the insertion of each antenna, a small spot at the summit of the orbit, the front of the scape and pedicel, a spot on the mandible, the palpi, the tegula, and usually the humeral angle of the pronotum and the upper margin of the mesopleurum beneath the tegula white or yellowish white. The type male is said to have two short white lines on the disc of the mesonotum. The tarsal claws are simple.

Material: 9 ♂, 10 ♀, from P. Q. (Stoneham), Me. (Mt. Katahdin), N. H. (Pinkham Notch), Mich. (Ontonagon Co.), and N. Y. (Bemus Point, Crystal Lake in Cattaraugus Co., Ithaca, Oneonta, Shokan, and Troy). Collection dates range from May 17 at Ithaca, N. Y., to Sept. 3 at Troy, N. Y. The type of *picticornis* is from N. J. and the types of *ornatulus* from

Aweme, Man., and Banff, Alta. Morley records this species from Nova Scotia and Hudson Bay. The type of *ornatulus* was bred from a tortricid pupal case.

This is evidently a northern species, not uncommon in the Canadian Zone but rare south of it.

Genus **Itoplectis** Foerster

Itoplectis Foerster, Verh. naturh. Ver. preuss. Rheinland. 1868. 25: 111. Genotype: *Ichneumon scanicus* Villers (= *Ichneumon maculator* Fabricius).
Nesopimpla Ashmead, Proc. U. S. Nat. Mus. 1906. 30: 180. pl. 13, fig. 3, n. syn. Genotype: *Nesopimpla naranyae* Ashmead.

The strongly emarginate eye, short malar space, black face (Nearctic species), and straight ovipositor distinguish this genus. Most of the species are structurally very similar and are therefore difficult to distinguish.

Nesopimpla differs from typical *Itoplectis* in lacking a basal tooth on the front tarsal claws of the female. This character does not seem of generic importance. Morley[16] has placed *Delaulax rufus* Cameron, the genotype of *Delaulax* Cameron, in *Itoplectis*. Mr. J. F. Perkins who has examined the type of *Delaulax rufus* informs me that *Delaulax* is a genus close to *Xanthephialtes* Cameron and *Ephialtes* Gravenhorst and that it includes a number of African species.

KEY TO SPECIES OF ITOPLECTIS IN EASTERN NORTH AMERICA

1. Front tarsal claws of female without a tooth; abdominal tergites with prominent eminences and depressions, entirely black; ovipositor sheath about 0.7 as long as petiole. (male unknown) ..... **brevacus**
   Front tarsal claws of female with a large tooth (fig. 7); abdominal tergites with moderate or weak eminences and depressions 2
2. Antenna clavate, the subapical segments fully as wide as long; middle tibia and tarsus and entire middle leg of male white; ovipositor sheath about 1.0 as long as the petiole ..... **clavicornis**
   Antenna filiform or slightly thickened toward the end, the subapical segments longer than wide; middle tibia and tarsus of female white, distinctly annulate with darker, middle leg of male with at least the femur largely ferruginous; ovipositor sheath about 1.8–2.0 as long as the petiole 3
3. Abdominal tergites with a distinct white band along the hind margin; abdomen narrower (third tergite of female about 1.6 as wide as long, that of the male about 1.0 as wide as long); fourth and fifth tergites of male polished and with well separated punctures; hind coxa of male always red ... **conquisitor**
   Abdominal tergites without a distinct pale band along the hind margin or if the bands are present, they are tan instead of whitish; abdomen broader (third tergite of female about 2.0–2.2 as wide as long, that of the male about 1.8 as wide as long); fourth and fifth tergites of male mat and with crowded punctures; hind coxa of male often more or less black 4
4. Last segment of hind tarsus entirely black; humeral corner of pronotum white; abdominal tergites often with brownish-white apical margins; anterior basin of petiole occupying about 0.65 its length; third abdominal tergite of female about 2.2 as wide as long, that of the male about 2.0 as wide as long ..... **obesus**

[16]Ann. Mag. Nat. Hist. 1914 8th ser. 14: 410

Last segment of hind tarsus with a white band at its base; humeral corner of pronotum usually black; abdominal tergites usually blackish without even a brownish margin; anterior basin of petiole occupying about 0.5 its length; third abdominal tergite of female about 2.0 as wide as long, that of the male about 1.8 as wide as long..... **quadricingulatus**

Itoplectis brevacus new species

Female.—Wing 8.5 mm. Black. Underside of second and following flagellar segments obscurely ferruginous; palpi brown; humeral corner of pronotum and tegula white. Legs ferruginous; front coxa except tip and tip of hind femur above black. Hind tibia and tarsus white marked with black as follows: basal fifth and apical half of tibia, apical two-fifths of tarsal segments one to three, apical two-thirds of fourth segment, and all except the extreme base of fifth segment.

Antenna filiform, the subapical segments about 1.3 as long as wide; thorax unusually long; lower division of metapleurum polished with evenly distributed very weak punctures; intercubital veins slightly separated on the radius; tarsal claws of moderate size, those of the front tarsus simple; abdomen long, cylindrical, closely and coarsely punctate, and with the tergal eminences and depressions very strong; petiole 1.2 as long as wide at apex; ovipositor tapering from the base to a rather slender point, its sheath about 0.7 as long as petiole.

Male.—Unknown.

This species fits the descriptions of the European *Itoplectis curticauda* Kriechbaumer as far as they go, but none with which I am familiar state whether or not *curticauda* has a tooth on the front claw of the female. Seyrig[17] has carefully compared *curticauda* with *clavicornis* and since he mentions no difference in the tarsal claws, I assume that *curticauda* has the basal tooth.

Type: ♀, Bar Harbor, Me., VII–5–35 (U. S.).

Itoplectis clavicornis Thomson

Pimpla (*Itoplectis*) *clavicornis* Thomson, Opusc. Ent. 1889. 13: 1409. ♀

I sent a specimen of this species to Dr. A. Roman of the Swedish National Museum which he determined as *clavicornis* Thomson. This is the first record for the species outside of Europe.

Female.—Wing 6–7 mm. Black. Underside of scape and flagellum whitish, grading to pale orange at the tip; palpi white; humeral corner of pronotum and tegula white. Legs ferruginous; tarsi, most of tibiae, and other markings on front and middle legs whitish; second trochanter of hind leg whitish; hind tibia and tarsus white marked with black as follows: annulus on extreme base of tibia; apical third of tibia; the entire fourth tarsal segment; and the other segments with a black annulus at their apices as long as the fourth segment.

[17] Ann. Soc. Ent. France. 1932. 101: 118.

Head very large, wider than the thorax; eyes very large; malar space about 0.25 as long as basal width of mandible; antenna clavate, the subapical segments distinctly wider than long; lower division of metapleurum polished with a few weak punctures in its upper third; intercubital veins connate above; middle and hind tarsal claws long, sharp, bent at a right angle and furnished with a moderately large pocket; petiole flat, 1.6 as long as wide; third tergite 1.2 as wide as long; tergites rather closely and finely punctate; ovipositor sheath 1.0 as long as petiole. In the clubbed antenna, large eye, short malar space, large claws, long petiole and short ovipositor this species is like no other in the Nearctic Region.

Male.—Like the female except as follows: underside of entire antenna, except for an orange tinge toward the tip, white; front and middle legs entirely white; third tergite 1.1 as wide as long.

I have studied a series from Italy and find that these European specimens differ from American specimens by being perceptibly stouter and by having the base of the hind coxa black and the black markings on the hind tibia slightly more extensive. On these bases it would be possible to erect a subspecies for American specimens.

Material: ♀, Rhinebeck, N. Y., VII–27–07, C. R. Crosby (Cornell); ♂, 5 ♀, Ithaca, N. Y., V–23–36, H. Townes (Townes); ♂, 7 ♀, Ithaca, N. Y., VI–2–36, H. Townes (Townes, Swedish National Museum, U. S.). The Ithaca specimens were all swept from rank herbage in woods on the north side of Six Mile Creek between the first and second reservoirs.

This rare species is known also from Sweden, England, Ireland, France, and Italy. It has been reared from cocoons of Ichneumonidae (*Phobocampe confusa*), Braconidae (*Macrocentrus abdominalis*), and in the U. S. National Museum is a series bearing the label "ex cocoon *L. disparis*, Italy, Gipsy Moth Laboratory."

Itoplectis conquisitor Say

Cryptus conquisitor Say, Boston, J. Nat. Hist. 1836. 1: 232. ♀
Cryptus pleurivinctus Say, Boston, J. Nat. Hist. 1836. 1: 235. ♂
Cryptus conquisitor Leconte, Writ. of Th. Say Ent. 1859. 2: 689. ♀
Cryptus pleurivinctus Leconte, Writ. of Th. Say Ent. 1859. 2: 691. ♂
Pimpla conquisitor Riley, Ann. Rep. Ins. Mo. 1872. 4: 43, note.
Pimpla conquisitor Walsh, Trans. Acad. Sc. St. Louis. 1873. 3: 137.
Pimpla piclipes Walsh, Trans. Acad. Sc. St. Louis. 1873. 3: 135. ♀ (not Gravenhorst).
Pimpla conquisitor Comstock, Rep. Cotton Insects. 1879. p. 198–200.
Pimpla conquisitor Provancher, Nat. Canad. 1880. 12: 42.
Pimpla conquisitor Provancher, Faune Ent. Canada Hymen. 1883. p. 463.
Pimpla walshii Dalla Torre, Cat. Hymen. 1901. 3: 454. ♀
Pimpla conquisitor Fiske, N. H. Agr. Exp. Sta. Tech. Bull. 1903. 6: 189–198.
Apechtis conquisitor Morley, Rev. Ichn. Brit. Mus. 1914. 3: 32.
Scambus (*Itoplectis*) *conquisitor* Viereck, Hymen. Conn. 1916. p. 321.

Ephialtes (*Itoplectis*) *conquisitor* Cushman, Proc. U. S. Nat. Mus. 1920. 58: 347.
Ephialtes (*Itoplectis*) *temnopleuris* Cushman, Proc. U. S. Nat. Mus. 1920. 58: 350 ♀, n. syn.
Itoplectis conquisitor Cushman and Gahan, Proc. Ent. Soc. Wash. 1921. 23: 160.
Itoplectis conquisitor Criddle, Ann. Rep. Ent. Soc. Ont. 1921. 54: 17–18.
Ephialtes (*Itoplectis*) *conquisitor* Liu, unpublished thesis at Cornell Univ. 1926. p. 149–157.
Itoplectis conquisitor Crowell, Psyche. 1932. 39: 102.
Ephialtes (*Itoplectis*) *conquisitor* Schaffner and Griswold, Misc. Pub. U. S. Dept. Agr. 1934. 188: 142.

The above references give only the synonymy, references to taxonomic literature, and the more extensive accounts of the biology of this species. Many more are to be found in the literature on economic entomology, most of them merely host records. Mr. Cushman believes that his *Itoplectis temnopleuris* is the same as this species, the peculiar little grooves on the mesopleurum being abnormal and probably caused by some projection on the inside of the pupa of the host, *Papilio marcellus*. I have examined the paratype of *temnopleuris* and agree that it is *conquisitor*. It seems possible that the specimens described by Cushman as *Itoplectis temnopleuris* are the same as those reared from *Papilio marcellus* by J. B. Smith and recorded as *Pimpla annulipes* by Scudder (Butterflies of Eastern North America 1889, p. 1279).

Female.—Wing 3.5–12.5 mm. Black. Underside of flagellum brown; palpi except the basal segment whitish; humeral angle of pronotum and tegula white. Legs ferruginous except as follows: front coxa blackish at base; front tibia with a dusky spot just before the middle; front tibia and trochanters marked with whitish; tip of hind femur above blackish; hind tibia and tarsus white marked with black as follows: basal 0.2 and apical 0.4 of tibia; apical 0.35 of first and second tarsal segments; apical 0.5 of third segment; entire fourth segment; and apical 0.4 of last segment. Middle tibia and tarsus white marked like the hind tibia and tarsus, but with dusky ferruginous instead of black. Apical margin of abdominal tergites whitish, brownish at the sides.

Antenna filiform, the apical segments distinctly longer than wide; metapleurum polished, weakly punctured except on its lower third; intercubital veins connate above; petiole 1.0 as long as wide, its anterior basin occupying 0.5 its length; third tergite about 1.6 as wide as long.

Male.—Like the female except as follows: scape and pedicel beneath white; palpi entirely white; third tergite about 1.0 as wide as long; fourth and fifth tergites polished with well separated punctures.

Material: 80 ♂, 180 ♀, from Que. (Joliette and Montreal), Ont. (Salines and Waubamic), Me. (Mt. Katahdin at 4,800 and 5,100 ft.), Mass. (Dorchester, Melrose, Mt. Tom, Princeton, and Woods Hole), R. I. (Ashaway, Kingston, and Westerly), N. Y. (Barrytown, Bemus Point, Buffalo, Canadarago Lake, Elmira,

Farmingdale, Flat Creek, Hancock, Horton, Huntington, Ithaca, Keuka Lake, Little Genesee, Lockport, Malloryville, McLean, Millwood, Mt. McIntyre at about 5,000 ft., Mt. Whiteface at 2,000 to 4,000 ft., Oneonta, Oswego, Penn Yan, Peru, Portageville, Poughkeepsie, Rochester Junction, Rock City, Shokan, Spring Lake, Syracuse, Vandalia, Waterville, and Yonkers), Pa. (Arendtsville, Fairview, Lehigh Gap, Paupack, and Philadelphia), Va. (Falls Church), Mich. (Bay Co., Clare Co., East Lansing, Iosco Co., Keweenaw Co., Midland Co., Osclola Co., and Wayne Co.), N. Dak. (Fargo, Kindred, and Sully Hill National Park), Ill. (Urbana), Mo. (Columbia and Savana), Ark. (Baldwin,) Colo. (Fort Collins and Lake City at 8,700 ft.), Tex. (Bexar Co. and West Columbia), and Calif. (Sonoma Co.). Mr. Cushman tells me that specimens in the U. S. National Museum are from "nearly every state east of and on the hundredth meridian, eastern Canada, Montana, Colorado, and New Mexico, also Bermuda Islands. We have it from as far south as Brownsville, Tex., and as far north as Quebec." This species appears to be one of the commonest of its family east of the Rocky Mts. over the whole of the United States and southern Canada. The specimen recorded above from Sonoma Co., Calif., seems to be the only record from the Pacific Coast Region. The specimen from Lake City, Colo., has an unusual amount of black on its hind tarsus, the white annulus on the fifth segment being incomplete. I have collected the species at eighteen of the thirty-three New York localities recorded above and found it at least moderately common at each. At Ithaca, N. Y., I have specimens taken from May 3 to September 17. More autumn collecting would doubtless show that occasional specimens are on the wing well into October. It is most abundant in the shrubby undergrowth of rather open woods.

The species has been recorded as a parasite of the following Lepidoptera: Psychidae (*Thyridopteryx ephemeraeformis*), Epermeniidae (*Epermenia cicutaella*), Tortricidae (*Archips argyrospila, A. cerasivorana, A. fumiferana, A. rosaceana, Eulia pinaturbana, Evetria frustrana, Laspeyresia molesta, L. pomonella, Peronea hastiana* (?), *P. minuta, Polychrosis viteana, Sparganothis pettitana, Spilonota ocellana, Tortrix quercifoliana*, and *T. fervidana*), Pyralidae (*Acrobasis betulella, A. caryaevorella, A. caryalbella, A. indiginella, A. juglandis, A. kearfottella, A. nebulella, A. rubrifasciella, Diaphania hyalinalis*, and *D. quadristig-*

malis), Pterophoridae (*Oxyptilus periscelidactylus*), Geometridae (*Cingilia catenaria*, "*Ellopia*" *fiscellaria*, and *Ennomos subsignarius*), Lymantriidae (*Euproctis phaeorrhea*, *Hemerocampa leucostigma*, *Lymantria dispar*, and *Notolophus antiqua*), Noctuidae (*Alabama argillacea*, *Anomis erosa*, *Autographa brassicae*, and *Bleptina* sp.), Arctiidae (*Hyphantria cunea* and *H. textor*), Saturniidae (*Hemileuca lucina* and *H. oliviae*), Lasiocampidae (*Malacosoma americana*, *M. disstria*, and *M. fragilis*), Papilionidae (*Papilio marcellus*), and Nymphalidae (*Vanessa antiopa* and *V. cardui*). In addition there is in the Cornell collection a female bred from *Nematocampa filamentaria* (Geometridae) by J. M. Hawley at Waterville, N. Y. Outside the Lepidoptera, the parasite has been reared from the cerambycid *Onciderus cingulatus* and as a secondary parasite on Braconidae (*Apanteles melanoscelus* and *Rogas terminalis*) and on Ichneumonidae (*Hyposoter fugitivus*) living in lepidopterous larvae. *Theronia atalantae* is the most common secondary parasite of *Itoplectis conquisitor*. Other species recorded as secondary parasites are *Hyposoter fugitivus*, *Dibrachys boucheanus*, and *Collopisthus suborbicularis*.

The hosts from which *conquisitor* is most commonly reared are *Malacosoma americana*, *Thyridopteryx ephemeraeformis* and *Hemerocampa leucostigma*. It is the commonest parasite of *M. americana*, ten to seventy-five per cent of the pupae of which were observed by Fiske to be parasitized by it in New Hampshire. Liu records a parasitism of 14.84% and 14.62% at Ithaca, N. Y., in the outbreak years of 1924 and 1925 respectively. Criddle in Manitoba records *conquisitor* parasitizing about 20% of *Hyphantria textor* in 1923. He states further that "in shrubby or semi-wooded country its usual hosts appear to be *Malacosoma fragilis* and certain Tortricidae, all tent-building species. In the more wooded country it may attack the insects already mentioned but readily infests as alternatives both *Malacosoma disstria* and *Hyphantria textor*." According to him the parasite has two generations, the first dependent mainly on *Malacosoma* and the second on *Hyphantria textor*. Comstock states that it is an important parasite of the last brood of *Alabama argillacea*.

In the great majority of cases *Itoplectis conquisitor* is a primary parasite, but may upon occasion become secondary. Fiske states that the development from egg to adult takes about twenty days. (Liu gives nineteen to twenty-three days for

nineteen progeny of the same female.) Of this period about half is spent in the pupal stage. In New Hampshire with *Malacosoma americana* as host, the parasites emerge from June 20 to July 15, the males averaging four days earlier than the females and the parasite usually emerging about four days earlier than the moth. In the northeastern states it has at least two generations and overwinters in the host pupa.

Liu has made some interesting observations on the biology of this species at Ithaca, N. Y. He kept specimens in the laboratory and observed that mating occurred freely in a shell vial, especially when the male had been allowed to rest overnight. The female may sometimes resist the male by spreading her wings, thus making it impossible for him to reach the underside of her abdomen with his own. Mating lasts from 40 seconds to 48 minutes, the longer periods required after many previous matings on the same day. One male which was kept alive for thirty days on 40% honey solution mated with 32 different females, mating seven times with one female and twice with another. Oviposition occurs most readily upon freshly spun-up larvae. It requires 50–180 seconds, depending upon the degree of exhaustion of the female as the result of previous ovipositions. The ratio of females to males in two series of specimens bred from *Malacosoma americana* (19 and 77 specimens) was three to one. My own collections indicate that this is about the usual ratio of sexes in the field.

Johnston has observed the feeding and oviposition habits of the female. He reports that the female selects a fresh pupa or prepupa (of *Autographa brassicae*), inserts her ovipositor, works the ovipositor up and down with a pumping motion for usually 30–90 seconds, then feeds on the juices exuding from the puncture for about 60 seconds. Then she repeats the procedure either at the same or at a new puncture for several times. Liu has observed the feeding of females also. He states that the ovipositor is rotated rather than moved up and down. Johnston has observed that a single female may oviposit upon as many as six hosts in a day.

Crowell observed oviposition into a mature larva of *Pyrausta nubilalis* within its burrow in a cornstalk. This is an unusual observation.

Itoplectis obesus Cushman

Itoplectis obesus Cushman, Proc. U. S. Nat. Mus. 1917. 53: 467.
Ephialtes (*Itoplectis*) *obesus* Cushman, Proc. U. S. Nat. Mus. 1920. 58: 344.
Itoplectis obesus Keifer and Jones, Monthly Bull. Calif. Dept. Agr. 1933. 22: 387.

Female.—Wing 4.5–6 mm. Black. Underside of flagellum ferruginous toward the apex; palpi whitish; humeral angle of pronotum and tegula white; legs ferruginous except as follows: front coxa black with ferruginous stains at apex; indistinct external dusky spot near the base of the front tibia; dusky external stripe on the basal half of the middle tibia with a whitish annulus at its center; middle tarsus dusky ferruginous with basal third of first segment and basal fourth of second segment whitish; dusky spot at the tip of the hind femur. The hind tibia and tarsus are black marked with white as follows: second fourth of tibia; tibial spurs; basal third of first tarsal segment; and basal fourth of second and third tarsal segments. First tergite with the central fourth of the apical margin buff, the rest of the tergites with the entire apical margin buff.

Antenna very slightly enlarged toward apex, the subapical segments distinctly longer than wide; lower division of metapleurum polished with a few weak punctures on the upper half; petiole 1.1 as long as wide, its anterior basin extending 0.65 its length; third tergite 2.2 as wide as long.

Male.—Like the female except as follows: scape and pedicel sometimes whitish in front; most of front and middle coxa whitish; dusky markings on the front and middle legs paler; hind coxa usually and sometimes the front and middle coxae more or less black; antenna slightly thicker at apex; third abdominal tergite 2.0 as wide as long; fourth and fifth tergites mat with the punctures crowded, especially in the middle near the base.

This species is difficult to distinguish from the following and may not be distinct.

Material: 2 ♂, ♀, Ottawa, Ont., 1925 and 1929, K. E. Schedl (U. S.); ♂, Revelstoke, Selkirk Mts., B. C., July 8–13, 1905, J. C. Bradley (Cornell); 4 ♀, Robeson, B. C., Sept. 2 to Oct. 16, 1939, H. R. Foxlee (Townes); 2 ♀, Godman Springs, Blue Mts., Wash., 5,700 and 6,000 ft., VII–26–35, J. F. G. Clarke, reared from pupae of *Depressaria* (Townes). The type is from Wenatchee, Wash., where it was reared from a pupa of *Archips argyrospila*. Cushman records other specimens from Clark Co., Wash. (from *Tmetocera ocellana*); Duncan, B. C. (from *Archips fumiferana*); and from Summit, Placer Co., Calif. Keifer and Jones reared five specimens from *Anarsia lineatella* pupae at Yuba City, Sutter Co., Calif. The adults emerged between April 7 and April 29.

Itoplectis quadricingulatus Prov.

Pimpla 4-cingulatus Provancher, Nat. Canad. 1881. 12: 38. ♀
Pimpla 4-cingulatus Provancher, Faune ent. Canada. Hymen. 1883. p. 459.
? *Pimpla* (*Itoplectis*) *kolthoffi* Aurivillius, Bih. Svenska vet-akad. Handl. 1890. v. 15, pt. 4, No. 1, p. 29, ♂ ♀, n. syn.
Ephialtes (*Itoplectis*) *quadricingulatus* Cushman, Proc. U. S. Nat. Mus. 1920. 58: 344.

Ephialtes (*Itoplectis*) *leavitti* Cushman, Proc. U. S. Nat. Mus. 1920. 58: 345. ♀, n. syn.
Ephialtes (*Itoplectis*) *leavitti* Cushman, *in* Leonard, List Ins. of N. Y. 1928. p. 937.
? *Pimpla* (*Itoplectis*) *alternans kolthoffi* Roman, Ark. Zool. (Stockholm). 1931. v. 23A, No. 6, p. 3.
Itoplectis leavitti Proctor, Biol. Surv. Mt. Desert Region. 1938. 6: 406.

The description of *kolthoffi* applies very well to this species except for the statement that the male coxae are entirely black. Roman believes *kolthoffi* a northern variety of *I. alternans* of Europe and in this view may be correct.

Female.—Wing 4.5–8 mm. Black. Under side of flagellum slightly ferruginous toward the apex; palpi brown; tegula white. Legs ferruginous except as follows: front coxa black, more or less ferruginous at the apex; an indistinct external dusky spot near base of front tibia; dusky external stripe on basal half of middle tibia with a whitish annulus at its middle; middle tarsus dusky ferruginous with basal third of first segment and basal fourth of the second and fifth segments whitish; and a dusky spot at tip of hind femur. The hind tibia and tarsus are black marked with white as follows: second fourth of tibia; tibial spurs; basal 0.4 of the first and second tarsal segments and a narrow annulus at the base of the third and fifth segments. Abdominal tergites with the apical margins blackish or brown.

Antenna very slightly enlarged toward the apex, the subapical segments distinctly longer than wide; lower division of metapleurum polished with a very few weak punctures on its upper third; intercubital veins connate above; petiole 1.1 as long as wide, its anterior basin extending 0.5 its length; third tergite 2.0 as wide as long.

Male.—Like the female except as follows: under side of flagellum pale; palpi white; coxae vary from entirely red to entirely black. Antenna slightly thicker at apex; third tergite 1.8 as wide as long; fourth and fifth tergites mat with the punctures crowded, especially in the middle near the base.

This species is difficult to distinguish from the preceding and may not be distinct.

Material: ♂, Savonoski, Nasneki, Alaska, VII–27–19, J. S. Hine (Ohio); ♂, St. Peters, N. S., VIII–29–30 and VIII–30–30, R. E. Balch (U. S.); ♂, Cape Breton, N. S., VIII–?–26, A. H. MacAndrews, *ex Archips fumiferana* (U. S.); ♀, Ottawa, Ont., 1929, K. E. Schald (U. S.); ♂, ♀, Mt. Desert, Me., VI–11–36, *ex Ancylis floridana* ? on *Arctostaphylos uva-ursi* (U. S.). The type of *quadricingulatus* is probably from Quebec, those of *kolthoffi* from Greenland (Auleitsivik July 1 and Nunasarnausak June 19), and that of *leavitti* is from St. Johns, N. B. Cushman has recorded this species from Richfield Springs, N. Y., (X–14–88, coll. Pergande). Roman records *kolthoffi* from Lapland, north Finland and western Germany.

Two eastern species described in the genus *Pimpla* belong to genera not within the limits of Pimplini and have not yet been referred to their correct positions. They are:

Scambus hirticauda Provancher, n. comb.

Pimpla hirticauda Provancher, Addit. faune Canada. Hymen. 1889. p. 116. ♀
The type is a small teneral specimen such as is often collected in the spring. The legs of this species are colored as in *Scambus pterophori* Ashmead.

Enizemum petiolatum Say, n. comb.

Pimpla ? petiolatus Say, Boston J. Nat. Hist. 1836. 1: 224. ♂
Bassus tibialis Cresson, Trans. Amer. Ent. Soc. 1868. 2: 110. ♀, n. syn.
Enizemum tibiale Davis, Trans. Amer. Ent. Soc. 1895. 22: 27.

Say's description fits the male of this species perfectly. A neotype (♂, Otsego Lake, N. Y., VI–25–35, H. K. Townes) is hereby designated. It is in the author's collection.

THE BOOK OF FISHES, Edited by JOHN OLIVER LA GORCE, Vice President, Nat. Geogr. Soc. Pages 1–367, 443 Color Portraits, 102 Biographies and 162 Photographs. 1939. Size, 7 x 10¼ inches. Published by the NATIONAL GEOGRAPHIC SOCIETY, Washington, D. C. Price, linen bound, $3.50.

Our copy of this precious volume rests on the sitting-room mantel where also rest the remains of our twelve-year-old son Bruce's first real kill, a stuffed eleven-pound great northern pike. It is one of the sacred spots of our home.

The book, very attractive with its beautiful photographs and many colored illustrations, is the National Geographic Society's companion work to "The Book of Birds." The present volume is a series of eleven parts by nine writers. Each covers the fish and fishing resources of a particular area of the waters of North America. Practically all the main game and food fishes are beautifully illustrated and interestingly treated in the text.

For the sportsman many record catches are described, such as the five-hour fight to land a devilfish twenty-two feet across from tip to tip of fins, which weighed more than 3,000 pounds, the 730 pound blue marlin taken on a 24-thread line by Mrs. Henry Sears and the many struggles with giant tarpon. "Fishing in Pacific Coast Streams" is an interesting section with its review of the kinds of trout and salmon. "Sea Creatures of Our Atlantic Shores" introduces the lay reader to the interesting and brightly colored invertebrates, the shells, star fishes, crabs, worms, sponges, etc. "Treasures of the Pacific" is largely free advertising of the excellent sea-fishing along the shores of California. "Our Heritage of the Fresh Waters" deals with the basses and other inland game fish, also their more lowly relatives, the gar fish (an alligator gar seven feet long), the spoonbill "catfish" with its curious paddle beak, the various sturgeon, eels and such. The serious omission is the series of very gamy sunfishes found only in the fresh waters of North America. Some of these, such as the blue-gill, are among our gamiest smaller fish and give small boys and fly fishermen much sport. Another boy's fish is the Kentucky minnow, specimens of which, six to eight inches in length, will outfight any trout. The saw-toothed fresh-water herring is another scrappy fighter.

This volume can be recommended as the best general review of fishing in North America of which we know. It is especially good on game fishes and gives the amateur uniformly excellent colored pictures of practically all sporting and food fishes.—C. H. K.

THE NORTH AMERICAN EPHEMEROPTERAN SPECIES OF FRANCIS WALKER

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In his work, *List of the Specimens of Neuropterous Insects in the Collection of the British Museum, Part III, Termitidae-Ephemeridae*, Walker considered thirty-two species of ephemerids from North America. Twenty-two of these were believed to be new to science, while the other ten were species that had been described by Say, Pictet, and Burmeister. Walker had specimens which he assigned to two of these ten species. The other eight, which he discussed although he had no material to represent them, are: PALINGENIA PUELLA PICTET = *Campsurus puella* (Pictet), PALINGENIA LIMBATA GUERIN = *Hexagenia limbata* (Guerin), BAËTIS INTERPUNCTATA SAY = *Stenonema interpunctatum* (Say), BAËTIS ARIDA SAY = *Isonychia arida* (Say), BAËTIS VERTICIS SAY = *Potamanthus verticis* (Say), BAËTIS OBESA SAY = *Baetisca obesa* (Say), *Caenis hilaris* Say, and *Ephemera guttulata* Pictet. These eight species are not considered further in the present paper.

Later students of the Ephemeroptera, especially Eaton (1871 and 1883–1888), have synonymized many of Walker's species. During the last two decades, however, intensive research on the North American Ephemeroptera has resulted not only in the description of many new species but also in the revival of some of Walker's names that had previously been synonymized. In order to determine whether or not the present concepts of Walker's species are correct, it seemed advisable to compare recently collected material with his original specimens. Through the kindness of the authorities at the British Museum (Natural History), it was possible to do this during the summer of 1939. I wish particularly to thank Messrs. N. D. Riley, D. E. Kimmins, and Martin E. Mosely for their courtesy and helpfulness in connection with my visit to England and the British Museum (Natural History). Mr. Kimmins kindly made invaluable study preparations of several ephemerid genitalia.

As stated in the introduction to Walker's *List*, "the different individuals of each species contained in the collection are indicated by letters a, b, c, etc." Eaton, when he studied the various specimens, put a label on each pin giving Walker's determination and the letter which Walker had allotted each specimen. Thus, regardless of the subsequent disposition of the specimens by Eaton or other students, it is still easily possible to locate and recognize the actual individuals that Walker considered. In addition the original locality labels are on the pins as well as distinctively colored type labels which have recently been added by the British Museum (Natural History).

In order to present a comprehensive and clear picture of Walker's material, each of his species is discussed individually. The disposition of the species which appears correct in the light of present knowledge is given, as well as any other pertinent information. The synonymy that accompanies each species is not complete, but merely consists of that which is considered important to the present discussion.

Ephemera decora Walker = *Ephemera simulans* Walker

Ephemera decora Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 537, 1853.
Ephemera simulans Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 536, 1853. Eaton, Revisional Mono. Rec. Ephemeridae, part 1, p. 67, 1883.

Walker based his species upon a single individual from "Canada" that had been "presented by Dr. Barnston." In the Brit. Mus. Nat. Hist. there is a male imago that is labeled "Canada" and, in Eaton's handwriting, "*Ephemera decora* (Type) Walker." There is no doubt that Eaton's synonymizing of the species is correct. The specimen agrees in all respects with the present concept of *E. simulans*.

Ephemera hebes Walker = *Blasturus cupidus* (Say)

Ephemera hebes Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 538, 1853. Hagen, Syn. Neuropt. No. Amer., p. 39, 1861.
Baëtis ignava Hagen, Syn. Neuropt. No. Amer., p. 47, 1861.
Leptophlebia cupida (Say). Eaton, Trans. Ent. Soc., Lond,. part 1, p. 89, 1871.
Blasturus cupidus (Say). Eaton, Revisional Mono. Rec. Ephemeridae, part 2, p. 101, 1884.

Walker based his species upon a female subimago from "Newfoundland" that had been "presented by W. C. St. John, Esq." No specimen meeting all of these qualifications could be found in the Brit. Mus. Nat. Hist. Some person has written the word "unrepresented" under the name *E. hebes* in the Museum's copy of Walker's *List*. Hagen (1861), who visited the Museum in 1857 and studied the ephemerids, did not see any specimens of *hebes* Walker and his description of the species is taken from Walker. Eaton (1871 and 1884) questionably placed *E. hebes* in *cupidus* but did not say that he saw the specimen.

In the entire ephemerid collection at Walker's disposal, there was only one specimen recorded from Newfoundland. There is in the Brit. Mus. Nat. Hist. a *female subimago* that bears three labels: (1) "N-f-dland," (2) "45 Baetis," and (3) in Eaton's handwriting, "*B. ignava* (Type) Hagen." Walker (p. 571) listed his forty-fifth species of the genus Baëtis as *Baëtis?* ——, subimago. He considered *Ephemera angustipennis* Rambur as a synonym of this partially named species! Comparison of Walker's description with that of Rambur (1842, *Hist. Nat. Ins. Neuropt.*, p. 295) clearly shows that Walker's description and distributional data were derived from Rambur. Thus we can safely conclude that Walker did not have any specimens to represent his *Baëtis?* —— subimago. This is all the more apparent when it is noted that Walker listed all of his specimens by letter. Somebody mistakenly put the label "45 Baëtis" on the true type of *E. hebes* Walker. Hagen (1861, p. 47), doubtfully described *B. ignava*, utilizing the specimen from Newfoundland. This individual is clearly a female subimago of *Blasturus cupidus* (Say). *Ephemera hebes* Walker and *Baëtis ignava* are therefore, as Eaton (1884) indicated, synonyms of *B. cupidus* (Say).

Ephemera simulans Walker

Ephemera simulans Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 536, 1853.
Needham, Traver, Hsu, etc., Biology of Mayflies, p. 252, 1935.

The species was based upon a single specimen that had been collected on the "River St. Lawrence" and "presented by the Entomological Club." Walker did not indicate the sex or whether the specimen was a subimago or imago. The Brit. Mus. Nat. Hist. has a male subimago labeled "R. Foster, River St. Lawrence," and, in Eaton's handwriting, "*Ephemera simulans* (Type) Walker." The specimen fits Walker's description and unquestionably agrees with the present concept of the species. *E. simulans* is so distinctive and well known that a redescription of the type is unnecessary.

Palingenia bicolor Walker = *Isonychia bicolor* (Walker)

Palingenia bicolor Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 552, 1853.
Siphlurus bicolor (Walker). Eaton, Trans. Ent. Soc. Lond., part 1, p. 128, 1871. Revisional Mono. Rec. Ephemeridae, part 3, p. 221, 1885.
Chirotonetes albomanicatus Needham, N. Y. State Mus. Bull. 86, p. 31, 1905.
Isonychia bicolor (Walker). McDunnough, Canad. Ent., vol. 63, p. 161, 1931.

Walker based his species upon a single subimago but did not mention the sex. The specimen had been collected at "St. Martin's Falls, Albany River, Hudson's Bay," and "presented by Dr. Barnston." In the Brit. Mus. Nat. Hist. there is a female subimago labeled "Hudson's Bay" and, in Eaton's handwriting, "*Palingenia bicolor* (Type) Walker." Subimagoes, especially old specimens, are usually difficult to study. Comparison of the type with recently collected subimagoes and imagoes leaves no doubt, however, that the present concept of the species as given by McDunnough is correct. The type also substantiates McDunnough's conclusion that *I. albomanicata* (Needham) is a synonym of *I. bicolor* (Walker).

Palingenia concinna Walker = *Blasturus cupidus* (Say)

Palingenia concinna Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 553, 1853.
Leptophlebia cupida (Say). Eaton, Trans. Ent. Soc. Lond., part 1, p. 89, 1871.
Blasturus cupidus (Say). Eaton, Revisional Mono. Rec. Ephemeridae, part 2, p. 101, 1884.

Walker based his species upon a single specimen, a male imago from "Nova Scotia" that was in "Lieut. Redman's collection." There is in the Brit. Mus. Nat. Hist. a male imago labeled "N. Scotia Redman" and, in Eaton's handwriting, "*Palingenia concinna* (Type) Walker." Mr. Kimmins has prepared a study mount of the genitalia. A careful comparison of the specimen and especially its genitalia with recently collected individuals of *B. cupidus* confirms Eaton's conclusion that *P. concinna* Walker is a synonym of *B. cupidus* (Say).

Palingenia natata Walker = *Ephemera simulans* (Walker)

Palingenia natata Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 551, 1853.
Ephemera simulans Walker. Eaton, Revisional Mono. Rec. Ephemeridae, part 1, p. 67, 1883.

The species was based upon two female subimagoes which had been collected at "St. Martin's Falls, Albany River, Hudson's Bay" and "presented by Dr. Barnston." Two female subimagoes in the Brit. Mus. Nat. Hist. are labeled "St. Martin's Falls" and, in Eaton's handwriting, "*Ephemera natata* (Type) Walker." Careful study confirms Eaton's conclusion that the species is a synonym of *Ephemera simulans* Walker.

Palingenia nebulosa Walker = *Blasturus nebulosus* (Walker)

Palingenia nebulosa Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 554, 1853.
Leptophlebia nebulosa (Walker). Eaton, Trans. Ent. Soc. Lond., part 1, p. 89, 1871.
Blasturus nebulosa (Walker). Eaton, Revisional Mono. Rec. Ephemeridae, part 2, p. 103, 1884. Needham, Traver, Hsu, etc., Biology of Mayflies, p. 538, 1935.

Walker based the species upon two individuals which had been collected at "St. Martin's Falls, Albany River, Hudson's Bay" and had been "presented by Dr. Barnston." The original description was of a male. There are in the Brit. Mus. Nat. Hist. two male imagoes which are labeled "Hudson's Bay, St. Martin's Falls" and, in Eaton's handwriting, "*Palingenia nebulosa* (Type) Walker." Traver's description of the species agrees with the types. The present concept of the species seems adequate. Since the second specimen of the original pair is in better condition than the first, I have designated it as the lectotype.

Palingenia occulta Walker = *Hexagenia limbata occulta* (Walker)

Palingenia occulta Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 551, 1853.
Hexagenia occulta (Walker). McDunnough, Canad. Ent., vol. 59, p. 119, 1927. Needham, Traver, Hsu, etc., Biology of Mayflies, p. 269, 1935.

Walker had three individuals which he considered as belonging to the species. Apparently he utilized all three in the construction of his description. They had been collected in "Arctic America, between Lake Winnipeg and Lake Superior" and "presented by Sir John Richardson."

In the Brit. Mus. Nat. Hist. there are three subimagoes, a male and two females, which are labeled "Arctic America" and, in Eaton's handwriting, "*Palingenia occulta* (Type) Walker." The male was Walker's "a" specimen and the two females the "b" and "c" individuals.

Color and distinctness of the color pattern are the most important criteria available for the separation of the various geographical subspecies of the genus Hexagenia. Unfortunately, the colors of pinned subimagoes fade. The color pattern is also usually obscured by the fading and by the shriveling that take place. To some extent this has happened to the three subimagoes in question. Thus the venter of the male's abdomen is faded and discolored so that the color pattern as well as the original colors can not be determined. There are, however, certain salient features of this type specimen that can be distinguished. They are as follows: The genitalia are clearly of the limbata type. The clear cut color pattern with a large amount of yellow maculation which is typical of the true *limbata* is lacking. Instead there is a general tendency, especially on the dorsum of the abdomen, for the yellow areas to be suffused with ruddy brown. The lightly colored subdorsal areas of the abdominal tergites are relatively small. They are lacking in tergite one. In tergites two to seven they are present as slender elongated areas that progressively increase in size in the distal segments. All of these areas are completely surrounded by the ruddy ground color. In segments eight and nine the areas are more elongately triangular, being based on the anterior edge of the tergites. The posterolateral angles of the tergites are occupied by lightly colored areas. There are no dark spots in the disks of the meta- and mesothoracic wings. The metathoracic wings lack dark outer margins. I have designated the male as the lectotype.

Except for the usual sexual differences, the two female subimagoes agree closely with the male subimago. They were apparently collected on the same date and at the same place as the male. All unquestionably belong to the same subspecies.

Comparison of the type series with recently collected material clearly indicates that the present concept of *occulta* as set forth by McDunnough (1927) and Traver (1935), the latter giving *occulta* specific rank, is adequate and correct. As indicated by McDunnough the subspecies displays a considerable amount of variation, especially in the amount and intensity of the ruddy infuscation, the size of the lightly colored subdorsal areas of the abdomen, and the presence or absence of the dark outer margin of the metathoracic wing. The subspecies is found in immense numbers in the Great Lakes and their tributaries and in the St. Lawrence valley.

Palingenia pallipes Walker = *Blasturus cupidus* (Say)

Palingenia pallipes Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 553, 1853.
Leptophlebia cupida (Say). Eaton, Trans. Ent. Soc. Lond., part 1, p. 89, 1871.
Blasturus cupidus (Say). Eaton, Revisional Mono. Rec. Ephemeridae, part 2, p. 101, 1884.

Walker, in his original description of the species, described the female and also the subimago. He had available three specimens that

had been collected in "Nova Scotia" and which came "from Lieut. Redman's collection." There is in the Brit. Mus. Nat. Hist. a female imago whose three labels bear the following information: (1) "R," (2) "N. Scotia Redman," and (3) in Eaton's handwriting, "*Palingenia pallipes* (Type) Walker." A second female imago bears similar data except that it lacks the second label. A male subimago also lacks the second label. Careful study of the three specimens and also comparison with recently collected material confirm Walker's conclusion that they all belong to the same species, and also Eaton's decision that *Palingenia pallipes* Walker is a synonym of *Blasturus cupidus* (Say).

Paligenia viridescens Walker = *Hexagenia limbata viridescens* (Walker)

Palingenia viridescens Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 551, 1853.
Hexagenia viridescens (Walker). McDunnough, Canad. Ent., vol. 59, p. 118, 1927.
Needham, Traver, Hsu, etc., Biology of Mayflies, p. 275, 1935.

Walker described his species from a single individual, stating neither the sex nor stage of development. The specimen had been collected at "St. Martin's Falls, Albany River, Hudson's Bay" and "presented by Dr. Barnston." There is in the Brit. Mus. Nat. Hist. a female subimago labeled "St. Martin's Falls" and, in Eaton's handwriting, "*Palingenia viridescens* (Type) Walker."

Eaton considered the species to be a synonym of what is now known as *Hexagenia limbata* Guerin. McDunnough (1927) withdrew the name from synonymy and applied it to a darkly colored, northern population of the genus Hexagenia. Since it is so closely related to *occulta* and other subspecies of *limbata*, a complete redescription of the type follows.

In general appearance the specimen is darkly colored, especially so for a female and despite the fading due to time.

Fronto-clypeal area yellow; basal segment of antennae slightly darker; second antennal segment medium brown, shading to yellowish brown at the tip; flagellum brown. Vertex black, except for a small posteromedial area where head meets thorax and regions posterior to lateral ocelli, all of which are yellow. Pronotum blackish brown except posterolateral yellowish areas. Fore coxa yellow with distal posterior surface darker; fore trochanter brown; fore femur brown; fore tibia light brown; first, second, and third fore tarsal segments yellowish brown but darker distally; distal tarsal segment and claws black. Prosternum yellow except for brown colored ridge between coxae. Mesonotum brown with yellow lateral areas anterior to scutellum; posterolateral membrane between meso- and metanotum yellow. Mesopleura yellow with a brown streak of color from wing root to sternum. The brown diffuses laterally. Mesosternum blackish brown. Mesocoxa brown; trochanter and femur lighter. Tibia yellow tinged with brown; tarsal segments one, two, and three yellow but slightly darker at tips; distal tarsal segment and claws brown. Metanotum brown; metathoracic legs missing; metapleura yellow with streaks of brown color from wing roots. Metasternum blackish brown.

All longitudinal veins of mesothoracic wing, except A_1 and A_2, are brown shading to yellow at wing base; A_1 and A_2 entirely yellow; cross

veins purplish except in anal region. Wing membrane tinged with yellow in costal and subcostal areas; slight infuscations on cross veins in costa and subcostal areas, but lacking elsewhere. Metathoracic wings similar to mesothoracic wings except that they have a broad distal border of purplish black.

Abdomen darkly colored; color pattern obscured. Subdorsal, lightly colored, paired areas lacking on tergites one and two, scarcely visible on three and four, but distinct on five to nine inclusive. Except on tergite nine, where they are based on the anterior margin, these areas are completely surrounded by the dark ground color. Posterolateral yellow areas present on tergites one to eight inclusive; on segment nine lateral yellow area extends entire length of the tergite. Abdominal sternites yellow except that the anterior sternites are infuscated with the dark color of the metathoracic sternum and except that sternites eight and nine each has a dark medial streak. Length exclusive of cerci, 21.5 mm.; length of mesothoracic wing, 25 mm.; length of metathoracic wing, 11 mm.

McDunnough's concept of the species seems to be correct. The dark coloration and the almost complete absence of subdorsal, lightly colored abdominal areas, especially in the males, serve to separate the subspecies from all of its American relatives. Typical individuals of *occulta* can be separated easily from *viridescens*, but dark individuals are distinguished with great difficulty. Further study will probably show that these two subspecies hybridize freely where their ranges overlap.

Palingenia vitrea Walker = *Iron vitrea* (Walker)

Palingenia vitrea Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 555, 1853.
Heptagenia vitrea (Walker). Eaton, Trans. Ent. Soc. Lond., part 1, p. 143, 1871. McDunnough, Canad. Ent., vol. 56, p. 117, 1924. Needham, Traver, Hsu, etc., Biology of Mayflies, p. 365, 1935.
Rhithrogena vitrea (Walker). Eaton, Revisional Mono. Rec. Ephemeridae, part 4, p. 254, 1885.
Epeorus humeralis Morgan, Ann. Ent. Soc. Amer., vol. 4, no. 2, p. 105, 1911.
Iron humeralis (Morgan). McDunnough, Canad. Ent., vol. 56, p. 129, 1924. Canad. Ent., vol. 57, p. 189, 1925.

Walker based the species upon a single subimago that had been collected at "St. Martin's Falls, Albany River, Hudson's Bay" and "presented by Dr. Barnston." In the Brit. Mus. Nat. Hist. there is a female subimago labeled "Hudson's Bay" and, in Eaton's handwriting, "*Palingenia vitrea* (Type) Walker."

Walker's description is inadequate and unfortunately Eaton's redescription (1885) is also insufficient for accurate placement of the species. Subsequent workers have therefore been confused. Traver (1935) considers *vitrea* as "an undetermined species." A complete description is therefore presented.

The type lacks all legs on the right side of the body, and the abdomen, which has been broken from the thorax, is glued to a piece of cardboard.

Clypeus yellow; antenna (left one missing) and entire frontal area pale brown; a black line runs from base of eye to antennal base and

continues over antennal base; vertex yellow with central area slightly darker. Pronotum brown with an indentation on medial portion of posterior edge; prosternum yellow; a thin brown streak between pro- and mesosternum. Fore coxa yellow; a black streak extending from edge of pronotum along side of coxa; remainder of fore leg yellow except tarsi which are light brown; also dark medial and apical bands on fore femur; tarsal segment five longest, two and three subequal to one and about three-fourths as long as five; segment four shortest, about one-half of segment one.

Synthorax yellow with black spots on pleurae, especially above coxae. Meso- and metathoracic legs yellow; coxae with black spots; femora with dark medial and distal areas, the terminal areas being less intense; tarsi slightly darker than remainder of legs; tarsal joinings dark; two tarsal claws on each foot asymmetrical. Wings light grey, venation slightly darker; humeral cross vein black in posterior half; cross veins in pterostigmal space straight and not anastomosed; those before the bulla weak. Had the specimen reached the imaginal state, the venation would have been almost hyaline.

Abdomen shriveled and discolored, especially dorsally, due mostly to the presence of eggs. All sternites clear yellow with no markings. Medially the tergites are brownish black with darker, transverse, laterally extending bars on the posterior margins. These laterally extending bars swing forward slightly and almost reach the lateral margins of the tergites. Lateral regions of tergites yellow. These yellow areas are divided by the transverse posterior bars into a small posterolateral area and a large anterolateral area. Cerci missing. Length undeterminable; mesothoracic wing length, 11 mm.

The posteromedial indentation of the pronotum, the pigmentation of the humeral cross vein, the condition of the cross veins in the subcostal area, the tarsal claws, and the relative lengths of the fore tarsal segments all indicate that *vitrea* is a member of the genus Iron. In connection with the relative length of the fore tarsal segments, it should be remembered that the specimen is a subimago. The published relative lengths are for imagoes which are considerably different from those of the subimagoes.

A comparison of the type with recently collected material leaves no doubt that *Iron humeralis* (Morgan) is a synonym of *Iron vitrea* (Walker). Each of Morgan's specimens, collected at Ithaca, N. Y., has a lighter colored abdomen than the type. McDunnough (1925) has shown that the northern specimens of the species have darker abdomens than do more southern representatives. It is therefore to be expected that the type which was taken near Hudson's Bay should be dark. The light colored thorax of the type eliminates *I. suffusus* McD. from consideration as a synonym of *I. vitrea* (Walker). Likewise the large size (mesothoracic wing, 11 mm.) eliminates *I. rubidus* Traver and *I. punctatus* McD., both of which are smaller, as possible synonyms of *I. vitrea* (Walker).

Baëtis angulata Walker = *Hexagenia limbata viridescens* (Walker)

Baëtis angulata Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 564, 1853.
Hexagenia bilineata (Say). Eaton, Trans. Ent. Soc. Lond., part 1, p. 66 (partim). Revisional Mono. Rec. Ephemeridae, part 1, p. 50 (partim).
Hexagenia occulta (Walker). McDunnough, Canad. Ent., vol. 59, p. 120, 1927 (partim). Needham, Traver, Hsu, etc., Biology of Mayflies, p. 269, 1935 (partim.)

Walker based this species upon a single male collected in "Canada" and "presented by Dr. Barnston." In the Brit. Mus. Nat. Hist. there is a small male labeled "Canada" and, in Eaton's handwriting, "*Baëtis angulata* (Type) Walker." The specimen is well preserved except that in the abdomen the pigment bearing layer which lies immediately under the chitin has flaked away to some extent. A careful study of the eye size, the remaining abdominal color pattern and the coloration of the head, cerci and wings indicates that *angulata* Walker is a synonym of *viridescens* Walker instead of *bilineata* Say as indicated by Eaton, or *occulta* Walker as McDunnough and Traver have held.

Baëtis annulata Walker = *Siphlonurus alternatus* (Say)

Baëtis annulata Walker. List Neuropt. Ins. Brit. Mus., part 3, p. 567, 1853.
Siphlurus alternatus (Say). Eaton, Trans. Ent. Soc. Lond., part 1, p. 17, 1871. Revisional Mono. Rec. Ephemeridae, part 3, p. 219, 1885.
Siphlonurus alternatus (Say). Needham, Traver, Hsu, etc., Biology of Mayflies, p. 466, 1935.

Walker had a single male specimen from "Trenton Falls, New York" that was "presented by the Entomological Club." In the Brit. Mus. Nat. Hist. there is a male imago which is labeled "R. Foster, Trenton Falls, New York" and, in Eaton's handwriting, "*Baëtis annulata* (Type) Walker." The specimen is in excellent condition. Study of Walker's type, especially of the genitalia, confirms Eaton's opinion that *B. annulata* Walker is a synonym of *S. alternatus* (Say).

Baëtis basalis Walker = *Siphloplecton basale* (Walker)

Baëtis basalis Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 565, 1853.
Heptagenia basalis (Walker). Eaton, Trans. Ent. Soc. Lond., part 1, p. 139, 1871. Revisional Mono. Rec. Ephemeridae, part 5, p. 298, 1887.
Siphloplecton basalis (Walker). McDunnough, Canad. Ent., vol. 56, p. 128, 1924.
Siphloplecton basale (Walker). Needham, Traver, Hsu, etc., Biology of Mayflies, p. 441, 1935.

Walker described the species from a single individual collected at "Lake Winnipeg" and "presented by Sir John Richardson." There is in the Brit. Mus. Nat. Hist. a single male imago labeled "S. of L. Winipeg" and, in Eaton's handwriting, "*Baëtis basalis* (Type) Walker." Eaton's redescription as given in his *Revisional Mono.* is as good as can be derived from the type since it is in a poor state of preservation. All the legs are lost and the abdomen, although intact, was badly smashed at the time the specimen was collected. The present concept of the species as set forth by McDunnough (1924) and Traver (1935) is correct.

Baëtis canadensis Walker = *Stenonema canadense* (Walker)

Baëtis canadensis Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 569, 1853.
Heptagenia canadensis (Walker). Eaton, Trans. Ent. Soc. Lond., part 1, p. 138, 1871.
Ecdyurus canadensis (Walker). Eaton, Revisional Mono. Rec. Ephemeridae, part 4, p. 278, 1885.
Ecdyonurus canadensis (Walker). McDunnough, Trans. Royal Soc. Canad., vol. 19, sec. 5, p. 222, 1925.
Stenonema canadensis (Walker). Traver, Jour. Eli. Mitch. Sci. Soc., vol. 48, no. 2, p. 175, 1933.
Stenonema canadense (Walker). Needham, Traver, Hsu, etc., Biology of Mayflies, p. 307, 1935.

Walker described the species from a male that had been collected in "Canada" and "presented by Dr. Barnston." The Brit. Mus. Nat. Hist. has a male imago labeled "Canada" and, in Eaton's handwriting, "*Baëtis canadensis* (Type) Walker." The specimen is in good condition. The present concept of the species is correct. As indicated by McDunnough the individuals show considerable variation in the amount of dark infuscation particularly on the abdomen. Specimens from the southern part of the range of the species, especially those captured in the late summer, are often much lighter in coloration than are the more northern representatives. The type which was collected in Canada is dark and compares closely with material from Ottawa, Canada.

Walker also described a variety of *canadense*, which he based upon a single specimen from an unknown locality. The specimen is present in the Brit. Mus. Nat. Hist. and has been labeled "*Baëtis canadensis* var. (Type) Walker" by Eaton. It is in a very fragmentary condition, consisting only of the head and part of the thorax. The latter bears the pro- and mesothoracic legs, a complete meso- and metathoracic wing and a part of another mesothoracic wing. The coloration is much lighter than that of the true *canadense*. The black clypeal band of *canadense* is replaced by two dots. The specimen does not belong to *S. canadense* Walker, but probably is a representative of *S. frontale* Banks. Because of the condition of Walker's specimen, accurate identification can not be made.

Baëtis debilis Walker = *Paraleptophlebia debilis* (Walker)

Baëtis debilis Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 569, 1853.
Leptophlebia debilis (Walker). Eaton, Revisional Mono. Rec. Ephemeridae, part 2, p. 98, 1884. McDunnough, Canad. Ent., vol. 57, p. 169, 1925.
Paraleptophlebia debilis (Walker). Needham, Traver, Hsu, etc., Biology of Mayflies, p. 519, 1935.

Walker's brief description of the species was based upon a single female that had been collected in "Nova Scotia" and was in "Lieut. Redman's collection." A single female imago, still retaining her eggs and labeled according to the data given above, is in the Brit. Mus. Nat. Hist. McDunnough (1925), with the aid of Mr. Blair, has associated this type with the correct male. The present concept of the species as set forth by McDunnough (1925) and Traver (1935) is adequate and correct.

Baëtis fusca Walker = *Rhithrogena jejuna* Eaton

Baëtis fusca Walker (partim), List Neuropt. Ins. Brit. Mus., part 3, p. 568, 1853.
Heptagenia fusca (Walker). Eaton, Trans. Ent. Soc. Lond., part 1, p. 138, 1871.
(Non) *Baëtis fusca* Burmeister, Hand. Ent. Band 2, p. 800, 1839.
Rhithrogena jejuna Eaton, Revisional Mono. Rec. Ephemeridae, part 4, p. 252, 1885. McDunnough, Canad. Ent., vol. 58, p. 195, 1926. Needham, Traver, Hsu, etc., Biology of Mayflies, p. 380, 1935.

Walker based his species upon three specimens. Two of these, "a" and "b," had been collected at "St. Martin's Falls, Albany River, Hudson's Bay" and "presented by Dr. Barnston." The third individual came from "Nova Scotia" and belonged to "Lieut. Redman's collection." There are in the Brit. Mus. Nat. Hist. two specimens, a male imago and a female imago, which are labeled "Hudson's Bay" and, in Eaton's handwriting, "*Baëtis fusca* (Type) Walker." There is also a male imago which is labeled "Nova Scotia" and, in Eaton's handwriting, "*Baëtis fusca* (c) Type Walker." This must be Walker's third specimen. Eaton, in 1871, recognized that the "c" individual does not belong to the same species as the other two. It is clearly a representative of *Blasturus cupidus* (Say).

Walker's name *Baëtis fusca* (1853) was preoccupied by *Baëtis fusca* Burmeister (1839). Eaton (1885) therefore renamed and redescribed the species, utilizing only the two specimens from St. Martin's Falls. Since he did not judicate a type, the male is hereby designated as the lectotype.

The description of the species as given by Traver (1935) fits the type well except that the legs are bistre instead of "sooty" and the wing membrane is slightly darkened in the pterostigmal area.

Mr. Kimmins prepared a study mount of the type's genitalia, and it shows clearly that the penes do not narrow at the tip as indicated by Traver (1935, fig. 102) but are broad as in *Rhithrogena undulata* Banks (*ibid.*). The distal outcurving of the penes is quite distinct and separates this species from *R. impersonata* McD. *R. undulata* Banks from the southwestern part of North America will probably prove to be a geographical subspecies of *jejuna* which is northeastern in its distribution.

Baëtis fuscata Walker = *Ephemerella walkeri* Eaton

Baëtis fuscata Walker (partim), List Neuropt. Ins. Brit. Mus., part 3, p. 570, 1853. Hagen, Syn. Neuropt. No. Amer., p. 47, 1861.
(Non) *Baëtis fuscata* Stephens, Illust. Brit. Ent., Mandib., vol. 6, p. 66, 1835.
Ephemerella walkeri Eaton, Revisional Mono. Rec. Ephemeridae, part 2, p. 129, 1884.
Ephemerella bispina Needham (partim, imago non nymph), New York State Mus. Bull. 86, p. 43, 1905.
Ephemerella fuscata (Walker). McDunnough, Canad. Ent., vol. 63, p. 214, 1931. Needham, Traver, Hsu, etc., Biology of Mayflies, p. 600, 1935.

Walker based his species upon two specimens, an imago and a subimago. He gave a short and inadequate description of each. The material had been collected at "St. Martin's Falls, Albany River, Hudson's Bay" and "presented by Dr. Barnston." There are in the Brit. Mus. Nat. Hist. a male imago and a male subimago which are labeled "Hudson's Bay" and, in Eaton's handwriting, "*Baëtis fuscata* (Type)

Walker." The subimago, specimen "b" of Walker, is shriveled and distorted so that accurate placement is impossible. Eaton (1884) thought it belonged to Rhithrogena. He was probably correct.

The imago, specimen "a" of Walker, was designated by McDunnough (1931) as the lectotype. It is in a fragmentary condition, consisting of a small part of the head, mainly the dorsal part and the compound eyes; the thorax which still bears the left mesothoracic wing, the metathoracic wings, the right mesothoracic leg, the metathoracic legs, both of which are broken at the distal termination of the tibia; and the first two abdominal segments. McDunnough (1931), with the aid of Dr. K. G. Blair, correlated the type with recently collected material. Comparison of the type with specimens from North America confirms McDunnough's conclusions. The present concept of the species as given by McDunnough (1931) and Traver (1935) seems adequate.

As indicated by Eaton (1884), *Baëtis fuscata* Walker (1853) is a homonym of *Baëtis fuscata* Stephens (1835) and is therefore invalid in *entirety*. Hence *Ephemerella walkeri* Eaton becomes the valid name for the species.

Baëtis invaria Walker = *Ephemerella invaria* (Walker)

Baëtis invaria Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 568, 1853.
Ephemerella invaria (Walker). Eaton, Ent. Month. Mag., vol. 5, p. 87, 1868. Revisional Mono. Rec. Ephemeridae, part 2, p. 129, 1884. McDunnough, Trans. Roy. Soc. Canada, vol. 19, sec. 5, p. 213, 1925 (partim). Canad. Ent., vol. 63, p. 196, 1931. Canad. Ent., vol. 70, p. 24, 1938. Needham, Traver, Hsu, etc., Biology of Mayflies, p. 607, 1935.

Walker based the species upon three specimens collected at "St. Martin's Falls, Albany River, Hudson's Bay" and "presented by Dr. Barnston." The Brit. Mus. Nat. Hist. has three male specimens labeled "Hudson's Bay" and, in Eaton's handwriting, "*Baëtis invaria* (Type) Walker." McDunnough (1925) designated the "a" individual as the lectotype of which Dr. Blair made a balsam mount of the genitalia and the last eight abdominal segments. The second specimen agrees with the type in coloration and size. The third is lighter in color than are the other two. Unfortunately it is in a poorly preserved condition and can not be identified with certainty.

E. invaria (Walker) belongs to a closely related group of highly variable species. The chief criteria utilized for the separation of the imagoes of these species have been the genitalia, the coloration, and to a lesser extent the size. Although the concept of the species as outlined by Traver and especially by McDunnough is correct, the following characteristics of the lectotype seem sufficiently important to be re-emphasized.

The general color is reddish brown rather than brown. The fore femur and tibia are reddish golden brown; fore tarsi yellowish white. Meso- and metathoracic legs light yellowish white; wing transparent, with the longitudinal veins of both the meso- and metathoracic wings *light brown*. Cross veins colorless or almost so, and not dark as in *E. subvaria*. Tergites much more intensely and brightly colored than the sternites, but of same hue. Each of the first segments of the forceps

of the genitalia has an expanded distal end; the penes (fig. 1) have the typical shape of the entire invaria complex of species; the penes of the type have mediodorsally a number of spines that are ***bilaterally unequal***, two distoventral spines, and ***no medioventral*** spines.

The lack of medioventral spines is, as McDunnough (1938) stated, the best criterion for distinguishing ***invaria*** from the closely related ***rotunda***.

Fig. 1. Genitalia of *Ephemerella invaria*.

Baëtis tesselata Walker = *Stenonema vicarium* (Walker)

Baëtis tesselata Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 566, 1853.
Heptagenia vicaria (Walker). Eaton, Trans. Ent. Soc. Lond., part 1, p. 150, 1871.
Ecdyurus vicarius (Walker) (partim). Eaton, Revisional Mono. Rec. Ephemeridae, part 4, p. 280, 1885.
Stenonema vicarium (Walker). Traver, Jour. Eli. Mitch. Sci. Soc., vol. 48, No. 2, p. 174, 1933.

Walker based his species upon a subimago from "Nova Scotia" that was in "Lieut. Redman's collection." In the Brit. Mus. Nat. Hist. there is a female subimago labeled "N. Scotia Redman" and, in Eaton's handwriting, "*Baëtis tesselata* (Type) Walker." As Eaton (1871) indicated, the species is a synonym of *S. vicarium* (Walker).

Baëtis vicaria Walker = *Stenonema vicarium* (Walker)

Baëtis vicaria Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 565, 1853.
Heptagenia vicaria (Walker). Eaton, Trans. Ent. Soc. Lond., part 1, p. 150, 1871.
Ecdyurus vicarius (Walker) (partim). Eaton, Revisional Mono. Rec. Ephemeridae, part 4, p. 280, 1885.
Ecdyonurus vicarius (Walker). McDunnough, Trans. Royal Soc. Canada, vol. 19, sec. 5, p. 222, 1925.
Stenonema vicarium (Walker). Traver, Jour. Eli. Mitch. Sci. Soc., vol. 48, no. 2, p. 174, 1933. Needham, Traver, Hsu, etc., Biology of Mayflies, p. 334, 1935.

Walker based his species upon a single male from "North America?" which had been "presented by the Entomological Club." In the Brit. Mus. Nat. Hist. there is a male imago which bears no locality label but has a printed label "Ent. Club. 44–12" and another, in Eaton's handwriting, "*Baëtis vicaria* (Type) Walker." The concept of the species as

given by McDunnough (1925) and Traver (1935) is correct. The lectotype agrees with Traver's description of the species except for the following points: The meso- and metathoracic tarsi are brownish black instead of "yellowish red" and the fore tarsi are sepia brown. The costoapical area of the mesothoracic wing is tinged with red, especially in the proximal part. As McDunnough (1925) indicates, it is a "decidedly ruddier tinge" than that found in *S. fuscum* Clemens. The sternites are not "creamy yellow" but rather purplish brown with translucent diagonal dashes and submedial spots.

The species is closely related to *S. pudicum* (Hagen) from which it can be distinguished by the light colored scutellum, by the lack of dark pigmentation on the metathoracic wing margin and by the *moderate* ruddiness of the pterostigmal area of the mesothoracic wing.

Ulmer (1921, *Archiv. f. Natur.*, Band 87, Abt. A, Hft. 6, p. 252) mistakenly describes as the type of this species a specimen in Selys' collection that had been collected in Canada in 1859. The specimen that Ulmer saw does belong to *S. vicarium* Walker, but is not the type.

Caenis diminuta Walker

Caenis diminuta Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 584, 1853. Eaton, Revisional Mono. Rec. Ephemeridae, part 2, p. 147, 1885 (partim). McDunnough, Canad. Ent., vol. 63, pp. 257–58, 1931. Needham, Traver, Hsu, etc., Biology of Mayflies, pp. 648–9, 1935.

Walker described his species from a single male specimen collected at "St. John's Bluff, E. Florida" and "presented by E. Doubleday, Esq." There is in the Brit. Mus. Nat. Hist. a male imago labeled "St. John's Bluff—E. Fla.," and, in Eaton's handwriting, "*Caenis diminuta* (Type) Walker." The type is preserved perfectly. The present concept of the species as set forth by McDunnough (1931) and Traver (1935) is correct. McDunnough (1931) has redescribed the species. His description, and also that of Traver which was taken from McDunnough, does not completely agree with the type. The following differences and additions to their descriptions should be noted:

Tergites seven, eight, and nine uniformly light yellow with black stigmatic dots; tergite ten light yellow with black shading; all sternites uniformly light yellow; meso- and metathoracic femora with dark apical bands.

In addition to the new species which he described, Walker also redescribed two previously known North American species, but instead of utilizing the original descriptions of the authors or their type material, he based his descriptions upon material in the British Museum. Because of the subsequent history of these species, it seems advisable to touch upon them briefly.

Siphlonurus luridipennis Burmeister

Baëtis luridipennis Burmeister, Handbuch der Ent., Band 2, p. 801, 1839. Pictet, Hist. Nat. Ins. Neuropt., Ephemerines, part 2, pp. 192, 1842.

Siphlonurus luridipennis Burmeister. Ulmer, Entomolog. Mitteilungen, Band 15, pp. 223–225, 1926. McDunnough, Canad. Ent., vol. 58, p. 190, 1926.

(Non) *Baëtis luridipennis* Burmeister. Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 563, 1853.

(Non) *Heptagenia luridipennis* (Burmeister). Eaton, Trans. Ent. Soc. Lond., part 1, p. 149, 1871.
(Non) *Ecdyurus luridipennis* (Burmeister). Eaton, Revisional Mono. Rec. Ephemeridae, part 4, pp. 279–280, 1885.

Burmeister based his species upon a male and a female that had been collected by Zimmerman in "Carolina." Following Burmeister, the specimens were never seen by *any* student of the Ephemeroptera until Ulmer (1926) located the female. Walker (1853) had a male from "St. Martin's Falls, Albany River, Hudson's Bay" that had been "presented by Dr. Barnston." This specimen was questionably placed in *B. luridipennis* Burm. and a description of it given. In the Brit. Mus. Nat. Hist. there is a male imago from "Hudson's Bay" and labeled, in Eaton's handwriting, "*Baetis? luridipennis?* Walker Type." This is the male specimen that Eaton (1871) utilized in describing *H. luridipennis* (Burm.) and (1885) *E. luridipennis* (Burm.). It is in reality a representative of *Stenonema fusca* Clemens. Unfortunately all workers subsequent to 1885 attempted to identify Burmeister's species from Eaton's description, hence the resultant confusion and uncertainty that prevailed until Ulmer (1926) discovered Burmeister's type specimen.

Stenonema interpunctatum (Say)

Baëtis interpunctata Say, Jour. Acad. Nat. Sci., Phila., vol. 8, p. 41, 1839. Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 562, 1853.
Baëtis flaveola Pictet, Hist. Nat. Ins. Neuropt., Ephemerines, part 2, p. 186, 1843. Walker, List Neuropt. Ins. Brit. Mus., part 3, p. 559, 1853.
Heptagenia interpunctata (Say). Ulmer, Archiv f. Natur., Band 87, Abt. A, Hft. 6, p. 242, 1921.
Stenonema interpunctatum (Say). Traver, Jour. Eli. Mitch. Sci. Soc., vol. 48, no. 2, p. 178, 1933.

Walker doubtfully referred three specimens to *Baëtis flaveola* Pict. They had been collected at "St. Martin's Falls, Albany River, Hudson's Bay" and "presented by Dr. Barnston." Eaton (1871, *Trans. Ent. Soc. Lond.*, part 1, p. 149), who had available Pictet's type specimen of *B. flaveola* which came from Tennessee and also Walker's material, placed them all in *Heptagenia flaveola* (Pictet). Eaton (1885, *Revisional Mono. Rec. Ephemeridae*, part 4, p. 278) considered *Heptagenia flaveola* (Pictet) as a synonym of *Ecdyurus verticis* (Say). Ulmer (1921) showed that Pictet's *B. flaveola* was really a synonym of *Stenonema interpunctatum* (Say) and McDunnough (1926, *Canad. Ent.*, vol. 58, p. 186) showed that *verticis* Say really belonged to the genus Potamanthus.

In the Brit. Mus. Nat. Hist. there are two female subimagoes and one female imago which are all labeled "Hudson's Bay" and, in Eaton's handwriting, "*Baëtis flaveola* (Type) Walker." The imago belongs to *Stenonema luteum* Clemens, one subimago to *Stenonema rubromaculatum* Clemens and the other to *Heptagenia hebe* McD.

A NEW TRIMENOPON FROM PANAMA

(Mallophaga: Trimenoponidae)

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In the fall of 1938, Dr. L. E. Rozeboom, now of Johns Hopkins University, gave the writer a single female specimen of the genus *Trimenopon* Cummings 1913, family *Trimenoponidae* Harrison 1915, which he had collected from a laboratory guinea pig in Panama, and which he regarded as possibly belonging to a new species. After an examination of the literature of the family, the writer was convinced it was new.

The author wishes to thank Dr. G. F. Ferris for the loan of some type material of *Trimenopon jenningsi*, Dr. H. E. Ewing for checking this description with the material in the United States National Museum, and Dr. R. Chester Hughes for his assistance with this paper.

Trimenopon rozeboomi n. sp.

(Figs. 1–4)

Description of Female.—Length of head, 0.31 mm., thorax, 0.53 abdomen, 0.92 mm.; width of head, 0.49 mm.; thorax, 0.53 mm., abdomen, 0.69 mm.

Head (fig. 3) triangular, wider than long, and much wider across temples than across forehead. A large wide antennal fossa, sides of which form about a 90 degree angle. A rather deep incurve in region just below maxillary palps gives lateral margin a sinuate appearance. On dorsal aspect of each temporal angle, below antennal fossa, there are 1 long, 4 medium-length, and 13 small setae. Numerous short setae scattered over dorsum of head. Dorsally, a row of 15 medium-length setae on each side of mandibles extends along a faint occipital band to posterior margin, with the last two rather long and heavier than usual. Occiput fairly straight. Antenna (fig. 2) four-jointed, the fourth segment containing a pronounced sensory pit; a division of segment 3 by a transverse suture apparent. Three setae occur on apical angle of segment 1, four longer ones on apical angle of segment 2, and about 16 fine hairs, in two series of approximately 8 each, on the margin of the sensory pit.

Prothorax large, about same length as head, nearly twice as wide at anterior end as at posterior margin, with conspicuous expanded lateral margins. Dorsally, a row of six anterior medium-length setae and 2 posterior longer ones occurs along inside of each longitudinal chitinous band paralleling margin of thorax. Pterothorax about two-thirds as

long as prothorax, expanding at posterior margin to nearly same width as prothorax; abundantly supplied with setae, with a long one arising from margin of each posterolateral angle.

Abdomen (fig. 1) about same length as head and thorax combined. Posterior margin simple, broadly rounded, attaining a width greater than that of head. Entire abdomen very thickly beset with setae which occur in 3 transverse rows on each tergite and each sternite; on the former, setae in posterior series twice as long as in other two, on each sternite the longest and shortest are in anterior and middle rows respectively.

Legs (fig. 4) normal.

Type host and *Type locality.*—*Cavia cobaya*, Panama, October 4, 1934 (L. E. Rozeboom).

Type material.—One female will be deposited in the United States National Museum.

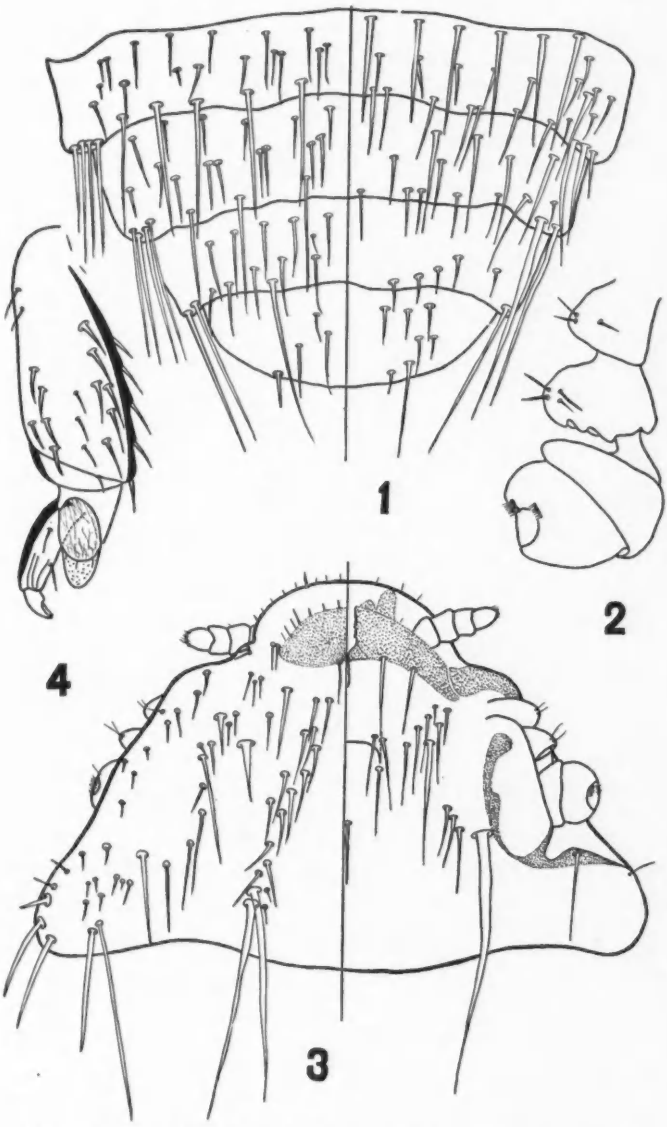
DISCUSSION

The early workers with this group—Kellogg and Nakayama 1914, Kellogg and Ferris 1915, Harrison 1916, Ferris 1922—recognized the genera *Philandesia* Kellogg and Nakayama 1914 and *Trimenopon* Cummings 1913, as being distinctly different. The separation was based upon two minor differences; in *Philandesia* the emargination of the dorsal expansion over the antennal fossa is deep and the temporal lobes are broad and rounded, whereas in *Trimenopon* the emargination is shallow and the temporal lobes are somewhat subangulate.

The author agrees with Werneck 1936 in regarding *Philandesia* as a synonym of *Trimenopon* since these differences are not enough to establish separate genera. This viewpoint is further enhanced by the new species which is distinctly intermediate between the two types.

Besides the new form, the genus now contains five valid species found principally on Central and South American Rodents, with only one from North America. They are (1) *Trimenopon jenningsi* (Kellogg and Paine 1910) from *Cavia cobaya*, (2) *Trimenopon mazzai* Werneck 1933 from *Eriomys chinchilla*, (3) *Trimenopon chinchilla* Werneck 1935 from *Eriomys chinchilla*, (4) *Trimenopon townsendi* (Kellogg and Nakayama 1914) from *Lagidium peruanum*, and (5) *Trimenopon foxi* (Ewing 1927) from *Marmota flaviventris*.

The new species can be distinguished from the rest of the species in the genus as follows: The thorax is smaller than that of *T. jenningsi*, while the abdomen is noticeably larger, and the



All figures concern female *Trimenopon rozeboomi* n. sp. and were drawn with the aid of a projection apparatus.

Fig. 1. Tip of abdomen, dorsal and ventral views. Fig. 2. Left antenna. Fig. 3. Head, dorsal and ventral views. Fig. 4. Right posterior leg.

head and thorax, both dorsally and ventrally, have many more setae; however, the head of *T. rozeboomi* is more nearly like that of *T. jenningsi* than any of the other species. On the tip of the female abdomen of both *T. mazzai* and *T. chinchilla* are groups of rather numerous long thick setae, which are not present in *T. rozeboomi*. The setae on the dorsal surface of the head of *T. mazzai* and *T. chinchilla* are more or less scattered without regularity, instead of being in definite rows. The head of *T. rozeboomi* does not have the ocular emarginations which occur in *T. townsendi*, and again the rows of setae on *T. rozeboomi* are not found on the latter form. The last segment of the female abdomen of *T. foxi* has a double comb of short, marginal setae, and a broad, truncate process on the second segment of antenna are not present on *T. rozeboomi*.

Characteristics of *T. rozeboomi* not found in any of the other species of the genus are as follows: two rows of setae on the dorsal surface of the head, each containing about 15 medium-length setae; three definite rows of setae on the dorsal surface of the abdomen; and the 16 sense hairs in two series of 8 each on the fourth segment of the antenna.

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THE NOMENCLATURE AND TAXONOMIC STATUS OF THE MOSQUITOES OF THE ANOPHELES MACULIPENNIS COMPLEX[1]

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The mosquitoes of the *Anopheles maculipennis* group have been the subject of many hundreds of papers since the publication, in 1920 and 1921, of the theories of Roubaud, Wesenberg-Lund, and Grassi to account for the absence of malaria in regions where *maculipennis* is abundant. Roubaud thought that there were two "physiological races," one adapted to feeding on man, the other on large domestic animals. Wesenberg-Lund thought that in Denmark the species had changed its food habits, becoming adapted to large domestic animals. Grassi, like Roubaud, thought there was a "biological race" that did not bite man. The search for the explanation of this problem of "anophelism without malaria" has made *maculipennis* one of the most thoroughly studied of all insects, and has uncovered a situation that is of considerable general biological interest from the point of view of the "species problem."

The history and bibliography of the basic work on the *maculipennis* problem has been covered in a paper by Hackett and Missiroli (1935). All students who have interested themselves in the problem seem to be agreed that the mosquitoes formerly included under the single taxonomic concept of "*Anopheles maculipennis*" form a group of more or less independent populations distinguished by various physiological and morphological characters. Beyond this fundamental point, however, there is little agreement. The various populations have been called "races," "biological races," "varieties," "biotypes," "subspecies," "species," and some twenty latinized names have been proposed for them. The object of the present paper is to review this situation from the points of view of taxonomy and evolution, and to determine to what category in the taxonomic hierarchy these populations should be assigned and what Latin names are available for denominating them.

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We shall first consider the definitions and general usage of the various taxonomic categories to which these populations have been at one time or another assigned (variety, species, etc.), and review very briefly the characteristics of the *maculipennis* populations in the light of these definitions. We shall then give brief histories of the various names that have been proposed in the synonymy of *Anopheles maculipennis* in the wide sense, and from these attempt to determine which names should be used for the various populations.

DEFINITIONS OF CATEGORIES

The following review is based largely on the chapter in Robson and Richards (1936) entitled "The categories of variant individuals." The names are taken up in alphabetical order.

Biotype.—Diemer and van Thiel (1936) have proposed that the *maculipennis* populations should be called biotypes; and they further organize the populations into "geobiotype-circles" more or less by analogy with the "Rassenkreis" principle. They define a biotype as "the organic structure type of all specimens, which have the same structure in the same stage of life and phaenotypically show only inconstant differences, which live in a coherent territory or in the same conditions of life, which in nature mate spontaneously and produce a perfectly fertile progeny."

The difficulty with this is that Diemer and van Thiel have taken a rather well-established term and redefined it to fit a particular case. The term "biotype" was apparently first proposed by Johannsen, and it is generally used to denote the least definable category of variant individuals. Du Rietz, for instance (1930, p. 340), has defined a biotype as a "population consisting of individuals with identical genotypical constitution." Thus, defined, biotypes are probably limited to asexual organisms and laboratory pure lines; but the term is sometimes applied to wild strains of sexual organisms, and it is a useful theoretical category (Robson and Richards, 1936, p. 72; Dobzhansky, 1937, p. 320). In this sense each of the recognized *maculipennis* populations seems to be composed of many biotypes, since diverse genetic strains appear to exist. This is most strikingly shown by the variation in larval pattern found associated with any particular egg-type, variation that seems to be genotypic rather than phenotypic.

Form.—The writer has used this term for the *maculipennis* populations in previous papers, considering that it conveyed no special implications concerning the status of the populations thus denominated. If the various "categories of variant individuals" are to be given more or less precise definitions, it would certainly be convenient to have some general term for populations or variations of undetermined status, and "form" might easily be reserved for this purpose. The same, of course, might be said of "variety," but variety to the writer, conveys a definite subspecific status that form does not. Form does, perhaps, imply a mor-

phological basis of separation, and in that way its use in situations like that presented by *maculipennis* is unfortunate. Du Rietz (1930, p. 342) has attempted to define form precisely as "a population of one or several biotypes occurring sporadically in a species-population (not forming distinct regional or local facies of it) and differing from the other biotypes of this species population in one or several characters." In that sense, the term "form" is, of course, quite inapplicable to the *maculipennis* populations.

Race.—From the very beginning of their study, the *maculipennis* populations have been called races, biological races, or physiological races more often than anything else. The term race is very often employed in biological literature, but it seems rarely to be defined. For the most part it is used as an exact equivalent of the more technical term "subspecies," and it is, in fact, defined in the dictionary (Webster) as "a natural group inferior in rank to a species." Like subspecies, the term "race" usually has a geographical connotation, and it is on "geographical races" that Rensch (1929) has constructed the "Rassenkreis" principle. Since the *maculipennis* populations are not always characterized by separate geographical ranges, they cannot be considered to be "geographical races," nor can the complex be considered to form a "Rassenkreis" in the sense of Rensch, although as Diemer and van Thiel have pointed out, some of the populations show "Rassenkreis" characteristics.

The term "biological race" has been defined by Thorpe (1930, p. 177), in his careful review of the subject, as follows: "A biological race may be said to exist where the individuals of a species can be divided into groups, usually isolated to some extent by food preferences, occurring in the same locality and showing definite differences in biology, but with corresponding structural differences, either few or inconstant, or completely absent." This definition would have applied admirably to the case of *maculipennis* at the beginning of its study; but the mass of evidence now accumulated seems to point to a much more profound cleavage between the *maculipennis* populations than would be indicated by such a definition. Most "biological races," in the sense of Thorpe, occur in phytophagous or parasitic organisms where a split in a species-population between two different hosts gives some chance of physical separation of the two resulting populations. The great divergence in habit between larva and adult in mosquitoes makes it difficult to conceive how the host association of the adult could result in physical (and subsequent physiological) separation in populations except where the alternative hosts belonged to separate habitats: and the habitat of man and his domestic animals is the same. The differences in the habits of the adults and larvae of the various *maculipennis* populations are relative, and it seems to the writer that they are much more readily explained as a *result* of the cleavage in the original population than as the *cause* of such cleavage. Any attempt at explaining the *maculipennis* populations in terms of biological races associated with different hosts is further complicated by the presence of at least seven such populations, although the only host difference so far suggested is between man and his domestic animals.

The term "physiological race" I take to be a simple synonym of "biological race."

Species.—Dobzhansky (1937, p. 306) has aptly pointed out that "in most animal and plant groups, except in so-called difficult ones, the delimitation of species is subject to no dispute at all." Yet no attempt at framing a definition of the term has met with any great success or general acceptance. This is partly due to the fact that although our knowledge of the vast majority of animal species is purely morphological, we mostly attempt to frame our definitions in physiological terms; and it is probably also partly due to the great variations in the behavior of organisms, which may mean that the characteristics of "species" in one group are different from those in another. The difficulty of framing a general definition, however, seems hardly a good argument for not defining the usage of the term for a particular group of animals. It is obviously out of the question to study the physiology of every putative species, to determine whether its characteristics fit those of a definition, and systematists will probably always continue to rely on analogy and inference—the inference that the behavior of an animal is different because its structure is different—in classifying their specimens. But since mosquitoes as a whole are probably the best known of all insect families, they might well serve as a basis for a careful study of the "species problem": of the nature of the physiological differences apt to be associated with differences in morphology.

Four definitions of species have been selected for consideration:

du Rietz (1930, p. 357): "The smallest natural populations permanently separated from each other by a distinct discontinuity in the series of biotypes, are called species. A species thus is a population consisting . . . of many sexually propagating biotypes forming a syngameon separated from all others by more or less complete sexual isolation or by comparatively small transitional populations."

Bates (1935, p. 70): "The general concept may be defined as a population or group of populations separated from other similar populations by some physiological barrier, which prevents fusion, and distinguishable by some heritable morphological characteristic."

Dobzhansky (1937, p. 312): " . . . . to define species as that stage of evolutionary process at which the once actually or potentially interbreeding array of forms becomes segregated in two or more separate arrays which are physiologically incapable of interbreeding."

Ginsburg (1938, p. 260): " . . . it is proposed tentatively to limit the designation of species and its subdivisions as follows: other things being equal, a given population is to be considered . . . a full species (with respect to another closely related population) when the degree of intergradation is not more than 10 per cent."

Ginsburg's definition is introduced as an example of an attempt to find an objective yardstick that can be used by taxonomists in their daily museum work. The common denominator of the other three definitions, and of practically all attempts at definition that have been made, is *sexual isolation*. The question of sexual isolation has been discussed at some length in the books by Robson (1928), Robson and

Richards (1936), and Dobzhansky (1937). In the case of free-living animal populations which are found in the same habitat at the same time, the presence or absence of sexual isolation can presumably be inferred from the morphological variation, by the presence or absence of a "distinct discontinuity in the series of biotypes." It is, of course, theoretically possible that two sexually isolated populations could occur in the same habitat without having any correlated morphological distinctions; but it would be very difficult to recognize such populations. The study of *Anopheles maculipennis*, for instance, made little progress until morphological distinctions were found. In comparing two populations from widely separated habitats or regions, we can usually only infer whether sexual isolation would be present or not, since the populations are already isolated by physical barriers. Most of the difficulties in species classification, in fact, arise from this latter case. It is not always possible to demonstrate sexual isolation by laboratory experiments, since the isolating mechanism in nature may depend on behavior patterns which are interrupted or lost in the laboratory.

It seems to the writer that the *maculipennis* populations, in the light of these definitions, must, in part at least, be considered to be "species." The reasons for this will be reviewed in a later section.

Subspecies.—The term "subspecies" is used in the taxonomy of the vertebrates and the Lepidoptera to designate a geographically defined and morphologically distinguishable population. The theory behind this usage is that it is only through geographical separation that a single animal population can become divided into two or more populations sufficiently isolated from one another to permit divergent evolutionary trends to set in. The evidence for this in the higher vertebrates and the Lepidoptera seems to be overwhelming (for a thorough review, see Jordan, 1905). Most attempts at formal definition of subspecies include this geographical concept: e. g., du Rietz (1930, p. 354), "A subspecies is a population of several biotypes forming a more or less distinct regional facies of a species."

It seems to the writer, however, somewhat presumptive to limit the general use of the term "subspecies" to populations definable in geographical terms, and in his review of the taxonomic units in Lepidoptera (Bates, 1935) he proposed to apply it to "any partially independent population considered to represent an evolutionary stage in the development of species." His idea was further to classify subspecies according to the isolating factors presumed to be in operation—geographical, ecological, and so forth. Remarkably little is known about the possible rôle of these isolating factors in the process of speciation in mosquitoes, although they would seem to be an almost ideal group for such study, because their general biology has been the subject of much investigation, and because many species can easily be kept for study as laboratory colonies. It seems quite possible that the most significant types of morphological and physiological variation in mosquitoes may be found to be correlated with geographical factors, as in the vertebrates and Lepidoptera; and if this is found to be the case, it should certainly be reflected in the nomenclatorial system.

Variety.—The *maculipennis* populations have been called varieties almost as frequently as races, and the two terms are alike in that they are non-technical English words with many connotations but without any very precise or generally accepted usage. In the Diptera the term "variety" is very generally used for any variant individuals that are not considered to represent "distinct species," and the use of the term for mosquitoes is simply a carry-over from this general practise of dipterists. This usage seems to be the result of the fact that, outside of *Drosophila*, practically no study of subspecific variation has been made in the Diptera, and most groups of flies are really so little known that such a study would hardly be profitable. The term "variety" is used in many invertebrate groups in this same sense, and Bequaert (quoted by Robson and Richards, 1936, p. 67) has defended this usage on the grounds that the word is "neutral," i. e., without any presumption as to the true status of the units as "geographical races," "individual aberrations," or "elementary species." In this sense the term is very useful, particularly if it is recognized as a sign that "more information is needed."

THE MACULIPENNIS POPULATIONS AS SPECIES

It may be worth while to recapitulate the points of difference between the *maculipennis* populations which seem to indicate a specific status. (The nomenclature used here is that of Hackett and Missiroli, 1935, and Bates and Hackett, 1939.)

MORPHOLOGICAL

Eggs.—We have found seven distinct types of eggs in the material that we have studied (Bates and Hackett, 1939, p. 1556) and in only two cases have we found intergrades and difficulty in classification: ***melanoon*** vs. ***subalpinus***, and ***typicus*** vs. ***messeae***. In the first of these two cases the distinction seems to be purely geographical, and eggs from intermediate geographical regions are intermediate in character, which would seem to indicate that the difference between the types was ***subspecific***. In the second case the confusion seems to be due to a phenotypic variation (due to temperature) which results in ***typicus*** eggs at certain times of year that are very similar to the eggs of ***messeae***. In general we have found the egg pattern and structure to be the most reliable and useful method of separating the ***maculipennis*** populations: and all of the other characters that have been found seem definitely to be correlated with these egg differences.

Larvae.—The branching of the antepalmate hair of the fourth and fifth abdominal segments seems to be characteristic for each population (Bates, 1939c), and it is often possible to identify individual larvae with some certainty (e. g., in Albania).

Adults.—The adults of ***sacharovi*** are readily distinguished from those of the other egg types by several characters (Corradetti, 1934). Yet ***sacharovi*** is an integral part of the ***maculipennis*** complex, as is shown by the results of hybridization experiments (Bates, 1939). Differences have been found in the male genitalia in the case of some of the pop-

ulations (Shute, 1935). Statistical differences in size, and in the maxillary index have also been found (Weyer, 1935).

PHYSIOLOGICAL

Sexual behavior.—As far as we have been able to study it, the epigamic behavior of the adults seems to be different in each population (Bates and Hackett, 1939, p. 1562) and the differences are of the same order of magnitude as those found between mosquito "species" in general.

Hybridization.—In the cases in which it has been possible to study hybrids, various degrees of sterility have been found in the F_1 generation (Bates, 1939), and in no case studied have the populations been found to be completely fertile *inter se.*

Physiological differences, correlated with the egg types, have been found in the larval ecology (Bates and Hackett, 1939), in larval survival in salt solutions (Bates, 1939b), in hibernation of the adults (Weyer, 1937), in the food reactions of the adults (van Thiel and Bevere, 1939). The *maculipennis* populations, in short, seem to show all of the physiological differences that one would expect to find in any group of related *Anopheles* species selected for study.

If we re-examine the four definitions quoted for "species," we find that the *maculipennis* populations have to be considered as "distinct species," in part at least, according to any of the four. They seem to be sexually isolated, and there are morphological differences in both egg and larva; only the adult is difficult to identify, and this is not true of one form (*sacharovi*).

The curious conservatism of the *maculipennis* adults under these circumstances deserves remark. Apparently morphological differences, although usually supposed to be correlated with "specific" physiological differences, are not necessarily present. One might suppose that the *maculipennis* populations are comparatively recently evolved species—and this is the usual supposition. But we know that in some cases insects have retained an identical morphological structure through long periods of geological time (e. g., the case of ants from Lower Oligocene amber identical in structure with ants living today. Wheeler, quoted by Robson and Richards, 1936, p. 132), and we know that mosquitoes are a comparatively ancient and conservative group of insects (Edwards, 1932, p. 6). The presence of mosquitoes with the *maculipennis* structure in America, Asia, and Europe would in itself indicate an ancient type, since there is no reason to suppose that this distribution has been brought about by man. It seems to the writer that it is very possible that the divergences in the *maculipennis* populations may have arisen in the geological past, and that perhaps originally each of the populations that we can now recognize occupied a distinct geographical range, the ranges merging only after the populations had diverged sufficiently to enable them to retain their identity when living together. At any rate, it would be very rash to use the present distribution of the *maculipennis* populations as an argument against the rôle of geographical isolation in the formation of species.

But after deciding that the *maculipennis* populations are species,

there remains the problem of nomenclature. Swellengrebel and de Buck long ago concluded that these mosquitoes were "species," but at the same time they thought that it would be a mistake to apply ordinary specific nomenclature to them. Their reasons (1938, p. 89) are weighty, and the writer was for a long time in agreement with them. The nomenclature of mosquitoes is already very involved and confusing, and no step likely to add to the confusion should be taken without careful consideration. Linnean nomenclature is essentially a tool—a fundamental tool in biological study—and its use depends on museum procedures which are concerned primarily with adult morphology. The *maculipennis* populations present well-defined morphological differences in the egg, but the study of these differences involves essentially biological procedures with the living animals: the eggs cannot be permanently preserved, and thus there is no possibility of "type specimens," and the comparison of material from different regions is very difficult. We might well restrict the Linnean nomenclature to cases that can be studied by museum procedures, and keep in mind that our Linnean species are, in part at least, only guide cards for filing our information.

The difficulty with this is that we are apt to forget that "*Anopheles maculipennis*" is an arbitrary concept not comparable, for instance, with "*Anopheles superpictus*." And it is very difficult to call "*atroparvus*" a variety of "*Anopheles maculipennis*" without beginning to think in terms of "elementary species" when, as we have seen, there is considerable evidence that the adjective "elementary" is entirely out of place. Swellengrebel and de Buck worked with a limited fauna with only two *maculipennis* populations, and their intention was to abandon Latin names for these populations altogether. This works admirably in the Netherlands, where they call their two populations "longwings" and "shortwings," but an extension of this system to the entire *maculipennis* complex would involve either the invention of a new set of names, or the removal of the present names from the system of zoological nomenclature; and neither of these alternatives is apt to gain very general acceptance. The present names have all been proposed in a Latin form as bona fide "subspecies" or "varieties," and while it is easy to shift such names from one category to another in the system, it is impossible to remove them once proposed—they would always remain in the synonymy.

If we give these *maculipennis* populations names like those we apply to any other mosquito species, it seems to the writer that the whole situation becomes much more intelligible. Swellengrebel and de Buck argue that people expect *Anopheles maculipennis* var. *atroparvus* to act the same way in, say, Hungary that it acts in the Netherlands, and that when a different behavior is found in Hungary, this is considered to throw doubt on the Netherlands observations. But would this be true if we thought in terms of "*Anopheles atroparvus*"? We are not surprised to find different behavior on the part of *Anopheles superpictus* in, say, Albania and Cyprus; and the difficulty in the case of *atroparvus* is not that we have fixed its attributes by giving it a Latin name, but that we are apt to restrict those attributes too narrowly ***because we have put the name in the wrong category.***

LIST OF AVAILABLE NAMES IN THE MACULIPENNIS GROUP

alexandrae (*shingarevi*) Shingarev, 1928.

Described as a subspecies of *maculipennis* on the basis of the male hypopygium; from the Vladimir and Penza Governments. Martini (1931, p. 163) gives a translation of the original description. It is generally listed as a synonym of *maculipennis* (Edwards, 1932; Zhelokhovtzev, 1937).

atroparvus van Thiel, 1927.

Described as a "variety" of *maculipennis* on the basis of the smaller size, larger number of maxillary teeth and dark color in comparison with the "typical" form found in Holland. This is the "shortwings" of Swellengrebel and de Buck. The type locality is Bolsward (Friesland). The "typical" form of van Thiel, the "longwings" of Swellengrebel *et. al.*, is the *messeae* of other authors.

aztecus Hoffmann, 1935.

Described as a subspecies (trinomial) of *maculipennis* on the basis of a number of morphological characters of larva and adult, which do not, unfortunately, allow comparison with the European forms. Hoffmann distinguishes two American "races," his *aztecus* and *occidentalis* Dyar and Knab; and in his 1936 paper he has given an extensive bibliography of these two names. The type locality of *aztecus* is the Valley of Mexico.

basilei Falleroni, 1932.

Proposed by Falleroni as a varietal name for the *maculipennis* laying eggs with two simple bars, which he and others had previously considered to be the "typical" form. The type locality of the name would presumably be Central Italy.

cambournaci Roubaud and Treillard, 1936.

Described as a variety of *maculipennis* from Portugal: like *atroparvus* but differing slightly in egg pattern and in behavior.

elutior Martini, 1931.

Described as a variety of *Anopheles elutus* from Turkestan, the description being based entirely on adult characters.

elutus Edwards, 1921.

Described as a new species of *Anopheles*, based on characters of the adult and egg, on material from various parts of the Near East, the type being from Kishon, Palestine. Edwards (1926) in the Italian edition of his revision of the Palearctic mosquitoes, placed this name in the synonymy of *sacharovi* Favr; but other authors have considered Favr's name to be of uncertain application, and have preferred to retain *elutus* (Martini, 1931; Hackett and Missiroli, 1935).

fallax Roubaud, 1934.

Described as a race of *maculipennis* from Normandy, based principally on characters of the egg. It is apparently a geographical or local form of *atroparvus*.

lewisi Ludlow, 1920.

Described as a new species of *Anopheles* from Siberia. It was placed in the synonymy of *maculipennis* by Dyar, and seems not to have been critically examined since.

maculipennis Meigen (1818, Syst. Beschr., I, p. 11; not seen).

By a process of elimination this name (*sensu stricto*) has come to be applied to the mosquito laying grey eggs with two simple bars: the *typicus* of Hackett and Missiroli, *basilei* of Falleroni. Hackett and Missiroli (1935, p. 93) give an historical sketch of the restricting process.

martinius Schingarev, 1926.

Described as a new species of *Anopheles*, based on characters of the adult, from Turkestan. Martini (1931, p. 164) suggested that it might be a variety of *Anopheles algeriensis*, but *Zhelokhovtzev* (1937), after an examination of the type, concluded that the name is a synonym of *sacharovi*.

melanoon Hackett, 1935.

Described in the paper by Hackett and Missiroli (1935) as a variety of *maculipennis*, based on characters of the egg. The distribution is there stated to be "north Italy, Tuscany, the region of Strasbourg, and the northeastern coast of Spain from Barcelona to Valencia." Later Hackett and Lewis (1935) in describing *subalpinus*, restricted the range of *melanoon* to Italy. Viareggio is specifically mentioned in the original description of *melanoon*, and perhaps this can be taken as the type locality.

messeae Falleroni, 1926.

Described as a variety of *maculipennis* based on egg pattern; probably, as in the case of *labranchiae*, the Pontine Marshes should be considered as the type locality.

occidentalis Dyar and Knab, 1906.

Described as a species of *Anopheles* from the western United States (type locality, Stanford University, California). Dyar himself subsequently considered this form to be identical with the European *maculipennis*.

pergusiae Missiroli, 1935.

Described as a variety of *maculipennis* from Sicily, based on characters of the egg. Missiroli has subsequently concluded that these eggs were merely aberrant examples of *labranchiae*, the common form in Sicily.

relictus Shingarev, 1928.

Described as a new species of *Anopheles* from Usbekistan, based on characters of the adult. Martini (1931, p. 146) gives a translation of the original description; both he and Edwards (1932) consider it to be a synonym or variety of *sacharovi*.

sacharovi Favr, 1903.

Described as a new species of *Anopheles* from the province of Elisabethpol (Caucausus). Edwards (1926, p. 271) has given a translation of the original description; he states that "it seems absolutely certain that this description corresponds to that of *A. elutus*. . . . I have examined many specimens from regions very close to that reported by Favr."

selengensis Ludlow, 1920.

Like *lewisi*, this was described as a new species of *Anopheles* from Siberia, and has subsequently been carried in the synonymy of *maculipennis*.

sicaulti Roubaud, 1935.

Described as a variety of *maculipennis* from Morocco, based on characters of the egg and adult behavior. It is very similar to *labranchiae*.

subalpinus Hackett and Lewis, 1935.

Described as a variety of *maculipennis* from Spain, northwest Italy, and Albania; based on characters of egg, larva, and adult genitalia. The statistics for larval variation given in the original description are based on Albanian material, hence this may be taken as the type locality.

typicus Hackett and Missiroli, 1935.

The first usage of this name in a Latin form seems to be in the 1935 paper of these authors. It is, by definition, an absolute synonym of *maculipennis* in the strict sense (*basilei*).

PROPOSED CLASSIFICATION OF THE MACULIPENNIS GROUP

Our own studies have been limited to the fauna of Albania and Italy, and consequently the following classification, especially in so far as it involves the Russian and American faunas, is purely conjectural.

Anopheles maculipennis Meigen

Syn.: *typicus* Hackett and Missiroli; *basilei* Falleroni.

This species is widely distributed in Europe, and it seems in general to be quite constant in its characters. To avoid possible confusion, the species could be referred to as "*maculipennis s. s.*," and the complex as the "*maculipennis* group."

Anopheles messeae Falleroni

The range of *messeae* corresponds quite closely with that of *maculipennis*, except that it does not extend as far south (e. g., it apparently does not occur in Greece). Southern records in the literature are apt to be unreliable, owing to confusion with *melanoon* and *subalpinus*.

Anopheles melanoon melanoon Hackett

Since *melanoon* is an older name than *subalpinus*, it must be used for the species, although *subalpnius* is a much more widely distributed form,

and the *melanoon* population is presumably derived from *subalpinus* rather than vice-versa. *Melanoon* seems to be limited to the Italian peninsula.

Anopheles melanoon subalpinus Hackett and Lewis

This form is found in Spain, northern Italy, and throughout the Balkans. The only known distinction between *melanoon* and *subalpinus* is in the egg, but the normal eggs are strikingly different, and intergrades seem to occur only in central Italy.

Anopheles labranchiae labranchiae Falleroni

Syn.: *pergusiae* Missiroli; *? sicaulti* Roubaud.

Labranchiae and *atroparvus* are much more distinct than *melanoon* and *subalpinus*, but at the same time they do not seem to be as distinct as, say, *subalpinus* and *maculipennis*, and it seems to the writer that this difference in level is best shown by making the two forms subspecies in the same "Rassenkreis." The ranges, as far as we know, overlap only in the vicinity of Foggia (Italy), and there no transitional forms have been found. The two subspecies are, however, partially fertile in the laboratory (Bates, 1939), and a hybrid colony was maintained in the Albanian laboratory for some time. *Labranchiae* seems to be limited to Italy, Spain, certain Mediterranean Islands, and north Africa.

Anopheles labranchiae atroparvus van Thiel

Syn.: *fallax*, Roubaud; *cambournaci* Roubaud and Treillard.

It seems likely that at most Roubaud's names indicate "local races" or perhaps even "biotypes" in the strict sense. *Atroparvus* is very widely distributed in central Europe, and it is in part broken into local populations by the discontinuity of its habitats, so that it is not surprising that many local variations should be found.

Anopheles sacharovi Favr

Syn. (all questionable): *elutior* Martini; *elutus* Edwards; *martinius* Shingarev; *relictus* Shingarev.

This is a Near Eastern form that has been studied carefully only in the vicinity of the Mediterranean coast: it is very possible that in other parts of its range it has broken up into distinguishable subspecies.

Anopheles occidentalis Dyar and Knab

It seems very likely that the American representatives of the *maculipennis* group may include several subspecies, or even species (*aztecus* Hoffmann). Perhaps *quadrimaculatus* Say should be considered as belonging to this group.

The following names must be considered as "of uncertain status": *alexandrae* Shingarev, *lewisi* Ludlow, *selengensis* Ludlow.

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THE PRINCIPLES OF HEREDITY, Second Edition, by LAURENCE H. SNYDER. Pages xv+452, 164 text figs. 1940. Published by D. C. HEATH AND COMPANY, 285 Columbus Ave., Boston, Mass. Price $3.50.

The new edition of this well-known and highly successful textbook appears in very different covers but with no important change in format.

The most valuable addition is Chapter XIX on Giant Chromosomes, a subject so recently developed that it has not received adequate treatment in textbooks of genetics. Other additions are a new nomenclature for modified two-factor ratios, a discussion of the chi-square concept, and problems to bring the total up to 502, consecutively numbered.

Although adverse criticism of details seems usually to give them unjustified emphasis in brief reviews, one detail here deserves such comment. The colored plate, Fig. 28a, for testing color-blindness, may be misleading. After a perfect test of a student for red-green color-blindness with the Ishihara test plates, the reviewer showed him this figure, which he read the same as a person with normal eyes! Everyone who knows the author will see in the combination of "onion" and "color" another example of his cleverly facile approach to the serious details of his teaching, but the printer's use of inks or paper seems to have played him false.

A point in which the book appeals strongly to the reviewer is that it is so distinctly what its title embraces, departing only in a brief chapter on eugenics and in interpolated comments on the evolutionary significance of some of the facts of heredity. With its clear typography, picking out important terms in bold-face, and its simple and intelligible presentation of materials, the new edition should retain the place so deservedly gained by the first as a leader in this field.—A. W. L.

THE EMERGENCE OF A NEOTROPICAL MANTISPID FROM A SPIDER EGG SAC[1]

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It is well known that prior to 1934, most of our information regarding the biology of the Mantispidae was based on the study of the European *Mantispa styriaca* Poda, published by Friedrich Brauer (1869). He gave *Lycosa inquilina* C. Koch as the host and mentioned finding a larva in an egg sac of a species of *Thomisus*. Other European records have been added to the host list, notably that of *Drassodes hypocrita* Simon by Poujade (1898), and a drassid spider of unknown identity by Main (1931).

The first record of the emergence of a North American mantispid was that reported by Smith (1934) in Kansas. He succeeded in having two pupae of *M. interrupta* Say emerge from egg sacs of *Philaeus militaris* Hentz [=*Dendryphantes marginatus* (Walckenaer)], but neither completed its development to the adult stage. Woglum (1935) reported *Plega signata* (Hagen) (=*Symphrasis signata* Hagen) from a pupa of a noctuid, *Xylomyges curialis* Grote, in California. The most recent North American emergence record has been published by Kaston (1938) who reared *M. fusicornis* Banks from the egg sac of *Agelena naevia* Walckenaer, specimens of which were originally collected in Michigan. Smith (1934) and Hungerford (1936, 1939) have been the outstanding contributors to our biological knowledge of the North American Mantispidae.

The literature does not appear to contain any definite rearing records of mantispids found in Central or South America. Apparently the only association of a neotropical species with host data is that of *Symphrasis varia* (Walker), which has been reported by Walker (1853) and Smith (1863) to have been found in nests of a vespid, *Polybia scutellaris* (White), taken in Brazil.

The writer wishes to express his appreciation to Dr. C. E. Mickel, of the University of Minnesota, for reading the manuscript and making valuable suggestions; to Dr. W. J. Gertsch, of the American Museum of Natural History, for identifying the host; and to Mr. John W. H. Rehn, of the Academy of Natural Sciences, for verifying the determination of the mantispid.

[1]Paper No. 1778, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul.

On October 3rd, a spider with its egg sac was taken from bananas in a grocery store in Minneapolis and brought to the entomological laboratory of the University of Minnesota. The egg sac was placed in a closed vial in order to determine whether or not it contained parasites. The spider was sent to Dr. W. J. Gertsch, of the American Museum of Natural History, who identified it as *Cupiennius sallei* (Keyserling) which is a member of the family Clubionidae. According to Dr. Gertsch, this is a very common species in Central America and one which has also been reported from parts of South America. It is highly probable that the bananas originated somewhere in Central America, although attempts to trace them were not successful.

A live male mantispid was observed in the vial on October 30th. It is not known exactly when the pupa left the egg sac or when the last moult occurred, but neither could have taken place much before the above date. Measurements of this interesting mantispid are as follows: Body 10 mm., front wing 11.3 mm. and hind wing 10 mm.; the entire length, including the wings, is 15.3 mm. The head is green except the front along the inner margins of the eyes, the vertex and the antennal segments beyond the second which are reddish and the eyes which are golden iridescent. The body is entirely yellowish green except indefinite light reddish markings on the pronotum and mesonotum; the legs are entirely green except the distal ends of the middle and hind tibiae and the tarsal segments which show some pale reddish color. The wings are green, iridescent, with only the costal vein and areas at forks of other veins being dark to blackish. In life, a distinct red pattern appeared along the whole length of the body, especially along the dorso-lateral regions of the pronotum and each of the abdominal segments. Soon after death these red markings disappeared entirely from the abdomen and faded considerably in the thoracic region.

The oval shaped cocoon, which measures 5 x 7 mm., is composed of loosely woven, pale yellow silk fibers. Emergence from the egg sac was accomplished by the active pupa through a circular opening 2 mm. in diameter. The length of the pupal exuviae is 8.5 mm. Extending along the dorsal line, from what were probably the forks of the epicranial suture nearly to the intersegmental membrane between thorax and abdomen, is the slit through which the adult emerged. The pupal prothorax is much shorter than that of the adult and resembles it very

little. Although the posterior wing pads are not as long as the anterior pair, they extend farther caudad, reaching a little beyond the middle of the third abdominal segment. Each of the second and third abdominal tergites bears a median fleshy tubercle-like structure, on which is located a pair of minute hooks on each side of the dorsal line; one hook of each pair is directed anteriorly, the other posteriorly. When the legs are drawn out all the parts become evident, as well as the "patella-like division" mentioned by Kaston (1938). Probably the most striking differences from the corresponding structures of the adult are the conspicuously shorter coxae of the fore legs and shorter femora and tibiae of the middle and hind legs. The distal segment of the middle and hind tarsi is much dilated; each tarsus bears a pair of simple claws.

The adult specimen runs in Enderlein's (1910) key to the subgenus *Mantispilla* Enderlein which is now considered to be of generic rank. In the keys published by Banks (1912) and Rehn (1939) it goes to *Mantispa* Illiger. Following a review of the various species which have been described or recorded from Central and South America, the specimen was tentatively determined as *Mantispa viridis* Walker, a species which apparently extends from Florida through Central America. This determination was verified by Mr. John W. H. Rehn, of the Academy of Natural Sciences, Philadelphia, who suggested that the species we are now calling *M. viridis* Walker may actually represent a complex of several species. Mr. Rehn is temporarily retaining the specimen for further study and intends to include it in a forthcoming revision of the genus *Mantispa*.

OBSERVATIONS OF THE LIVING SPECIMEN

During the period from October 30th to November 7th, when the mantispid died, observations were made of some of its habits. It was very active during the first few days and jumped about in the vial, especially when placed in direct rays of artificial light. The antennae were constantly kept in motion, very similar to many of the parasitic chalcids. Two drosophilid flies (*Drosophila ampelophila* Loew) were introduced into the vial in order to learn something of the type of food consumed and the feeding habits. At first, these small flies actually ran between the legs of the mantispid without being seized, and it required considerable time before the mantispid apparently realized that food was at hand. Two hours later, only the wings

remained as remnants of the flies. Several of these flies were later introduced on different days, and each time, the mantispid appeared alert and seized its prey almost immediately and with astonishing rapidity and accuracy. Ten to fifteen flies were consumed during the adult life. In all instances observed, it was noted that the head of the prey was the part first consumed, followed by the remaining parts, except the wings which were discarded. Flies were grasped in almost any position between the tibia and femur of the raptorial leg. After seizure, however, they were usually rotated or manipulated into a position that enabled the mantispid to begin feeding on the head of the prey. Either raptorial leg was used for capturing, but both were employed to manipulate the fly, provided it was not in a suitable position for feeding.

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LONGEVITY AND EGG PRODUCTION IN THE COMMON BEAN WEEVIL, ACANTHOSCELIDES OBTECTUS (SAY)[1]

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Reproductive activity and duration of life are two biological variables which play important roles in the economy of any species. The relationships between them have not only broad biological significance but also, in many cases, considerable economic importance. Hence detailed studies of reproduction and longevity in particular species are of general as well as specific interest. The common bean weevil (*Acanthoscelides obtectus* (Say)) has proven to be a highly satisfactory species for such studies; its reproductive activity can be measured by egg counts and its duration of life in days. Since relatively few data on these biological variables are available for insects, we present here a summary of the features of egg production by mated and unmated females and longevity of mated and unmated individuals. The results are analyzed statistically and compared with those of similar studies reported for other insects.

METHODS

The stock of *Acanthoscelides obtectus* from which the individuals used in these experiments were taken was one which had been maintained on white navy beans under laboratory conditions for about four years. It is believed that only a small amount of inbreeding had occurred, because new mass cultures were always started with twenty or more individuals.

For individual observations the weevils were sexed in the adult stage. This is easily accomplished by examining the pygidium, which in the male has a median ventral curvature into the hypopygidium readily visible under the binoculars. No such curvature is visible in the female, the hypopygidium being approximately of the same width from side to side. Also aiding in the distinguishing of the sexes is the

[1]This investigation was conducted at the University of Georgia.

fact that the female, as a rule, is somewhat larger than the male. The distinguishing features of the two sexes are shown in Figure 1.

By isolating infested beans at regular intervals from the stock cultures it was possible to secure individuals within 24 hours after emergence. Care was exercised to select beans infested with only a few individuals so that the effects of crowding during development would be eliminated, since excessive crowding within the host bean had been observed to reduce the size of the adult weevils emerging therefrom. The effects of this factor on longevity and fertility are being made the object of a separate investigation.

Two ounce salve boxes (Labelid) proved to be efficient containers for the weevils under observation. These boxes can be stacked easily and take up a small amount of space. The white eggs are readily visible

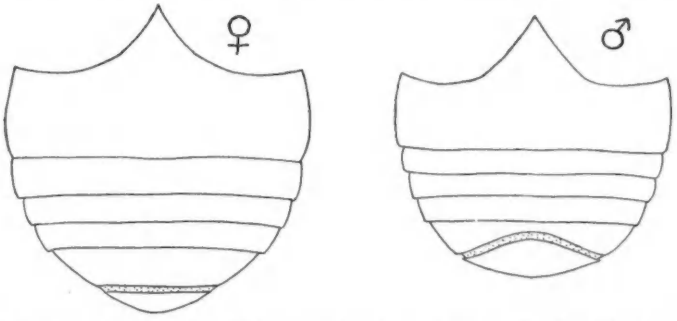

Fig. 1. Ventral views of the abdomens of male and female *Acanthoscelides obtectus* showing the curvature of the pygidium of the male. Male on right, female left.

on the bottom of the boxes. The latter are large enough to provide satisfactory circulation of air, especially so, when the boxes are opened daily for examination of eggs and adults. The daily record can be kept on the top of the box. In routine procedure each box is provided with three white navy beans under which the female deposited her eggs.

The beetles were reared at room temperature and, as adults, were kept in an incubator at approximately $27 \pm 1°$ C. Humidity was not controlled; however, the relative humidity probably never ran over 50 per cent. The adults were provided with no food or water and there is no evidence that they obtained either from the beans. As far as the authors were able to determine this species does not feed on the dry bean after pupation.

The present work includes observations on the following:

a—100 unmated males, one male to the box.
b— 76 unmated males, two males to the box.
c—110 mated pairs, one male and one female to the box.
d— 74 unmated females, one female to the box.

In routine observations on unmated males (a and b) it was necessary only to examine daily to determine the day of death. In the case of the females, daily counts of the eggs were made. To facilitate counting,

the daily batch of eggs could readily be removed. If for any reason it was desired to retain all the eggs laid by any one female frequent transfers of the weevils to clean salve boxes made egg counting easier.

Unfertilized eggs of the common bean weevil invariably collapse and flatten out within twenty-four hours after being laid. Such eggs are characteristic of the unmated females. Collapsed, presumably unfertilized, eggs may also appear toward the end of the ovipositional period of the mated females. In our records no distinction is made between normal and unfertilized eggs as far as the number of eggs is concerned.

LONGEVITY

The data on length of life are summarized in Table I. It will be noted that there is a slight tendency for the unmated males and females

TABLE I

LENGTH OF LIFE

	N	Mean (days)	C. V.	Range (days)
Mated ♂♂	110	16.6 ± 0.2	20.2 ± 1.4	7–29
Unmated ♂♂ (alone)....	100	17.3 ± 0.2	18.1 ± 0.9	11–26
Unmated ♂♂ (2 per box)	76	17.8 ± 0.2	16.4 ± 0.9	7–24
Mated ♀♀	110	16.8 ± 0.2	16.9 ± 0.8	8–25
Unmated ♀♀	74	17.3 ± 0.2	16.2 ± 0.9	12–24

to live longer than mated males or females. However, the differences are not great enough to be significant statistically except for the unmated males kept two in a box. The difference between the length of life of the latter and that of the mated males is four times the probable error of the difference. There is not much difference in the relative variabilities for length of life in the different groups.

EGG PRODUCTION

The data on the total egg production per female are summarized in Table II. Mated females lay significantly more eggs than do unmated

TABLE II

TOTAL EGG PRODUCTION

	N.	Mean	C. V.	Range
Mated ♀♀	110	44.2 ± 0.9	31.7 ± 1.5	10–75
Unmated ♀♀.....	74	28.2 ± 1.0	44.3 ± 2.5	3–55

females. The difference is approximately twelve times its probable error. The mated are less variable than the unmated ones with respect to the total number of eggs laid. The mated females laid 1.56 times as many eggs as did the unmated ones.

The mean number of eggs laid by mated females in our experiments is considerably lower than the average given by Menusan ('35) for females ovipositing at 27.1° C. and 90 per cent relative humidity. The difference between our results and those of Menusan is probably due to the fact that in our experiments the relative humidity probably never ran over 50 per cent., a condition, which Menusan shows, results in a lower average egg production on the part of the female bean weevils.

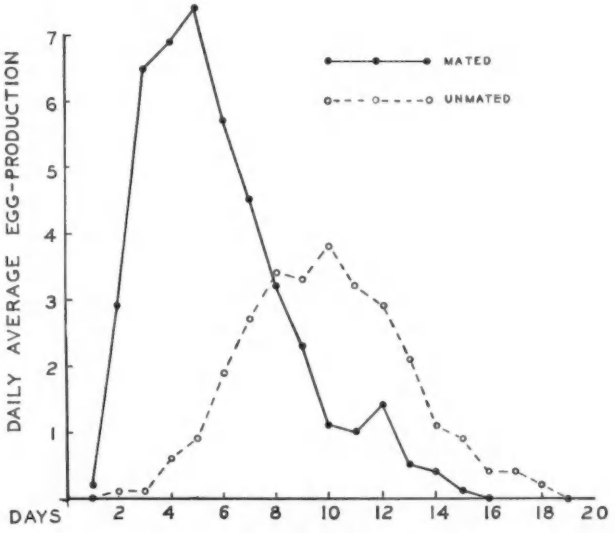

Fig. 2. Curves of average daily egg production for mated as compared with unmated females.

RATE OF OVIPOSITION

A very marked difference in the rate of egg laying exists between the mated and unmated females. Figure 2 represents graphically the average daily egg production of all the mated females (solid line) as compared with that of the unmated ones (broken line) throughout their lives. The mated females lay a large number of eggs starting with the third day of their existence, the peak of their production being reached on the fifth day after emergence. The daily egg production gradually tapers off after the fifth day for mated females. The unmated females tend to withhold their eggs and the curve climbs more slowly, the peak being reached the twelfth day after emergence. The mated females at their peak laid an average of 7.4 eggs in one day, whereas the unmated

females at their peak, on the twelfth day, laid an average of 3.8 eggs. All the mated females had completed their egg laying by the end of the sixteenth day; the unmated, by the end of the nineteenth day.

PERIODS OF FEMALE ADULT LIFE AS RELATED TO EGG PRODUCTION AND LONGEVITY

The shapes of the curves for average daily egg production suggest a further analysis based on the three periods of female adult life; these are: *pre-oviposition*al, *oviposition*al, and *post-oviposition*al. The analysis of the data is presented in Table III. It is evident that the *pre-oviposition*al period is significantly longer for the unmated females (Table III, A). The difference in the duration of the *oviposition*al period is not

TABLE III

ANALYSIS OF VARIOUS PHASES OF FEMALE ADULT LIFE OF THE BEAN WEEVIL AND HER OVIPOSITIONAL RATE

			Mean	C. V.	Diff. (M. & V.)	Diff. / P.E. diff.
A	Pre-oviposit. period (days)	M*	1.6 ± 0.1	69.6 ± 3.3	3.4 ± 0.2	17.0
		V**	5.0 ± 0.2	38.2 ± 2.2		
B	Oviposit. period (days)	M	9.4 ± 0.2	27.3 ± 1.3	0.8 ± 0.3	2.7
		V	8.6 ± 0.2	31.4 ± 1.7		
C	Post-oviposit. period (days)	M	5.8 ± 0.2	45.1 ± 2.2	2.3 ± 0.3	7.7
		V	3.5 ± 0.2	69.8 ± 3.8		
D	Actual No. days on which eggs were laid (days)	M	7.1 ± 0.2	23.8 ± 1.1	0.6 ± 0.2	3.0
		V	6.5 ± 0.1	17.2 ± 1.0		
E	Average daily output for oviposit. period (eggs)	M	4.9 ± 0.1	36.1 ± 1.7	1.5 ± 0.2	7.5
		V	3.4 ± 0.2	51.0 ± 2.8		

*Mated females (N = 110).
**Unmated females (N = 74).

great for the two groups, being only 0.8 days in favor of the mated females (B). The *post-oviposition*al period is significantly shorter for the unmated females. It is evident that although the unmated females spend approximately the same number of days laying eggs, their egg-laying period is markedly delayed as compared with that of the mated females.

In both the mated and unmated groups there are differences among individual females in regard to the number of days during the oviposition-al period on which eggs are laid. A difference of 3 times its probable error is shown for the mean number of such days for the two groups (Table III, D).

As will be brought out later, there is a relationship between the rate at which the females lay their complements of eggs and their total life spans. For the determination of this relationship the data were analysed by dividing the total number of eggs produced by the number of days occupied in laying them for each of the females. This is called the average daily output for the ovipositional period. (It cannot be considered a true rate as can be seen from figure 1 because that rate would be high early in life and become progressively smaller as the individual grows older). As shown in Table III (E) there is a significant difference in favor of the mated females. The mated females are also less variable in this respect than are the unmated, as was the case, also, for the total egg production.

EGG PRODUCTION IN RELATION TO LONGEVITY

The data were analysed in order to detect a possible relationship between egg production and length of life of the females. The results are presented in Table IV. For mated females there is no significant correlation between total duration of life and total egg production (Table IV, A). A slight positive correlation is evident for the total duration of life of the unmated females and their total egg production (A), possibly because these individuals tend to withhold their eggs and those that live longer have more time in which to lay. (It is evident from Table II that the unmated females probably rarely deposit their full complement of eggs).

The duration of the *pre-oviposition*al period shows a small negative correlation with total egg production for both the mated and the unmated groups (B). Seemingly, then, there is either a tendency to forego completion of egg laying by females which are late in starting, or, possibly, those having a lower egg laying capacity also begin laying later. The *pre-oviposition*al period shows a small positive correlation with length of life (E). The duration of the *oviposition*al period is positively correlated with total egg production in both the mated and unmated groups (C). Females which are to deposit large numbers of eggs will take a greater number of days for egg laying. Both mated and unmated females tending to oviposit over a long period of time also tend to live longer as is shown in the positive correlation between total duration of life and the duration of the ovipositional period (F). If we examine the relationship between the actual number of days on which eggs were laid to the total duration of life, we see that there is still a good positive correlation (I). The average number of eggs laid per day over the *oviposition*al period is negatively correlated with the total duration of life for both mated and unmated groups of females (H). A similar relationship was found for *Drosophila melanogaster* by Alpatov ('32). Female bean weevils and Drosophila laying their eggs in larger batches over a shorter period of time are apt to survive only for a short time. The duration of the *post-oviposition*al period in both the mated and unmated females is positively correlated with the total length of life (G). There is a small negative correlation between the duration of the *post-oviposition*al period and the total number of eggs produced by

the mated females; no such correlation is indicated between these two entities in the case of unmated females (D).

The correlation coefficient for total eggs of the female and the life of her mate is -0.020 ± 0.064; that for the life of the female and life of her mate is $+0.167 \pm 0.062$.

TABLE IV

CORRELATION COEFFICIENTS FOR VARIOUS PHASES OF LIFE AND EGG PRODUCTION OF FEMALE BEAN WEEVILS

		Mated	Unmated
A	Total life (days) vs. Total eggs	$+0.062 \pm 0.063$	$+0.172 \pm 0.076$
B	Pre-oviposit. period vs. Total eggs	-0.284 ± 0.059	-0.298 ± 0.070
C	Ovipositional period vs. Total eggs	$+0.362 \pm 0.055$	$+0.259 \pm 0.070$
D	Post-oviposit. period vs. Total eggs	-0.169 ± 0.062	$+0.088 \pm 0.077$
E	Pre-oviposit. period vs. Total life	$+0.125 \pm 0.064$	$+0.062 \pm 0.080$
F	Ovipositional period vs. Total life	$+0.344 \pm 0.056$	$+0.477 \pm 0.065$
G	Post-oviposit. period vs. Total life	$+0.637 \pm 0.038$	$+0.492 \pm 0.061$
H	Ave. daily output of eggs for oviposition period vs. Total life	-0.207 ± 0.061	-0.196 ± 0.077
I	Actual No. days on which eggs were laid vs. Total life	$+0.250 \pm 0.060$	$+0.462 \pm 0.060$

DISCUSSION

The results of our studies on *Acanthoscelides obtectus* in general accord with, but differ in detail from, the observations reported for two other species of insects, *Drosophila melanogaster* and *Trichogramma evenescens*. A brief comparison follows:

Duration of Life. For Drosophila, Hanson and Ferris ('29) found that virgin females, on the average, have a life span 14.8 days longer

than the mated females. Our results show only a slightly longer life span for virgin females of Acanthoscelides. However, because of the shorter life span of the bean weevil (about 17 days) as compared with that of Drosophila (about 42 days for mated and 59 days for unmated females, according to Hanson and Ferris), one could not expect to find such outstanding differences between mated and unmated groups without using shorter intervals of comparison. Larson and Fisher ('38) found that unfed mated individuals of the bean weevil lived an average of 16.0 days and unfed unmated individuals lived an average of 16.9 days.

For *Trichogramma evanescens* Lund ('38) found that isolated males and isolated females tend to live longer than mated males and females if all were unfed; the difference is entirely erased if all are fed. He suggests that pairing results in an increased expenditure of energy, which shortens the life of unfed individuals. Our data show no significant shortening of life due to pairing. When two males of the bean weevil are kept together, however, there seems to be a tendency toward a longer life than is characteristic of either isolated males or females. This might suggest a lower energy expenditure on the part of unmated males confined in pairs.

Egg-production. For Drosophila, Hanson and Ferris ('29) found that the peak of egg laying is reached much earlier by mated than by virgin females. Our results with Acanthoscelides agree. For purposes of comparison egg-production curves for the bean weevil and for Drosophila (based on the data given by Hanson and Ferris for mated and virgin white-eyed flies) were computed. The number of eggs produced up to certain given periods (single days for Acanthoscelides and 5-day intervals for Drosophila) of the life span are expressed as percentages of the total number of eggs laid. The curves are shown in figure 3. For mated females (solid lines) of both species the egg-production curve rises sharply and then levels off as the insects become older. In the case of the unmated females, however, the rate is lower at first, and the rise in the curve continues almost to the end of life. Alpatov ('32) collected available data on the oviposition rates of several insects and showed that for many of them the rate is well expressed by the logistic curve.

As regards the numbers of eggs laid by mated and unmated females, Hanson and Ferris ('29) report that mated females of Drosophila lay from 1.63 to 2 times as many eggs as do virgins. These authors also state that Rau's data on egg laying by cecropia moths show that mated females produce 1.67 times as many eggs as do unmated females. For our data on the bean weevil, egg-production of mated females is 1.540 times that of the unmated. For *Trichogramma* Lund ('38) found that mated females produce fewer progeny than do virgin females. It is conceivable that this special characteristic may be associated with the parthenogenetic habits of this species.

Egg-production and Longevity. From the theoretical standpoint egg-production in relation to length of life might be considered from two angles. The laying of a large number of eggs might represent an inherent vitality on the part of the female which could conceivably express itself also in a prolonged life. On the other hand, heavy egg-

production might be considered as a strain upon the organism which would result in the shortening of life. A marked positive correlation between total eggs and length of life would be suggestive of inherent vitality; a marked negative correlation would suggest a strain on the female due to heavy egg-production. To differentiate between these two possibilities in a heterogeneous population is a difficult task. The genetic factors involved in egg-production and in longevity may prove to be quite independent, so that correlations based on observations of mixed strains might very likely obscure relationships which actually do exist within the strains involved. Selection of strains on the basis of egg-production and of duration of life is being undertaken at the present time with the hope that the relationships which are reported here for the species can be compared at a later date with those existing within selected strains.

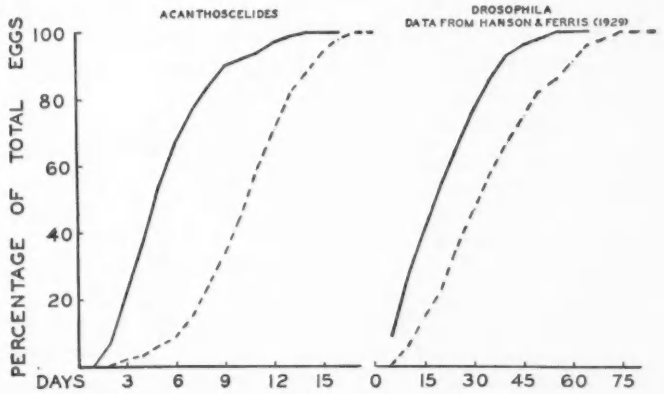

Fig. 3. Cumulative percentage curves of the egg production of the bean weevil and of Drosophila as related to age.

For the bean weevil the correlations between total eggs and total life are insignificant. Alpatov ('32) reports a negative correlation between length of life and the average egg-production per day for Drosophila. Our results for the bean weevil are in harmony with this finding. There is a significant negative correlation for these two factors in both the mated and the unmated classes. This relationship is expressed also in the positive correlations between length of life and the duration of the ovipositional period. Long lived females, then, tend to lay smaller batches of eggs over a longer period; this apparently conserves energy in living as well as in egg laying. Our results show further that the longer the duration of the pre-ovipositional period, the lower will be the total egg-production of the female.

Lund ('38) reports a significantly high correlation between longevity and egg production for the mated females of Trichogramma.

SUMMARY

1. Duration of adult life for mated and unmated male and female bean weevils, *Acanthoscelides obtectus* (Say), as well as total egg production and rate of egg-laying for mated and unmated females was studied.

2. Mating has a pronounced effect on both the total egg production and the stimulus to early laying. The beginning of egg-production is delayed for an average of 3.4 days in the case where the female remains unmated. Mated females lay an average of 1.54 times as many eggs as unmated ones. Unmated females lay eggs which collapse soon after having been laid.

3. Males and females are about equal in longevity. No significant differences for longevity among the different groups is found except for unmated males (kept two in a box) as compared with mated males and females.

4. No significant correlation, either positive or negative, between total egg production and duration of adult life of mated females is found, but there is a small positive correlation between these two characters in the case of unmated females. A good positive correlation exists between the length of the ovipositional period and the total egg production, and also between ovipositional period and the total duration of life, for both mated and unmated females. A negative correlation is found between duration of life and average egg production per day during the ovipositional period.

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TWO MACROPSIS FROM TEXAS
(Homoptera: Cicadellidae)

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Macropsis breakeyi n. sp.

Greenish brown with definite dark markings on pronotum, scutellum and elytra; males darker than females, epimera unmarked. Differs from *M. nigricans* (V. D.), which it resembles, by its smaller size and unmarked epimera.

Male.—Vertex almost parallel margined, narrower midway between apex and eyes. Pronotum with anterior margin rounded; rugae coarse, infuscate, median line poorly defined; anterior impressions extending irregularly from lateral margins a little more than half distance to center of anterior margin; posterior margin with shallow, scarcely angulate sinus. Scutellum punctate on disc, surface of apical area transversely striate. Elytra broadly rounded apically, long; veins somewhat pale, but not distinct. Face tumid, especially before lorae, when viewed from side; rugae and punctures slightly infuscate, indistinct. Clypeus short, swollen, widened at base, sides straight to rounded apex, sutures obsolete, lorae and genae but narrowly exposed. In female, clypeus short, swollen, sides rounded, broader at base, apex rounded, and sides indented before apex; lorae swollen.

Color: Greenish fulvous to greenish brown above, markings dark brown. Pronotum with coarse rugae, darkened, the anterior impressions spotted and stained with dark brown; scutellum greenish fulvous, a dark brown triangle within each basal angle, a pair of short, stout, brown transverse dashes before median transverse impression. Elytra subhyaline to hyaline on outer third, deep brown coloring encircling an oval pale area included, except for apex, in apical half of claval area. Dark color emphasized anterior and posterior to this pale area on the claval suture, and on apices of elytra. Below pale greenish yellow, with lateral anterior areas of pygofers in males darkened, also abdominal tergites, and some darkening, but no distinct spots on sternite below anterior femora.

Male.—Length, 4.5 mm., width 1.5 mm. *Female.*—Length 5 mm., width 1.5 mm.

Male holotype, allotype, 34 male and 12 female paratypes. collected in Davis Mts., Texas, Sept. 20, 1938, by D. J. and J. N. Knull, from *Salix* sp., and deposited in the collection of The Ohio State University.

The species is named for Dr. E. P. Breakey who has done careful work in this genus.

Macropsis davisi n. sp.

Somewhat resembling *M. hesperia* Breakey, but with epimera of males unmarked and clypeus swollen in both sexes.

Male.—Vertex narrowly parallel-margined, subangulate apically; pronotum obtuse-angled before, convex, anterior impressions particularly deep, and longer than long diameter of eye, rugae inconspicuous, median line hardly discernible; posterior margin with shallow, scarcely angulate sinus. Scutellum impunctate, impressed median line deep. Elytra long, broadly rounded at apex. Face tumid, clypeus swollen, margins obscure. Pygofer with stout brown apical spines visible from ventral view. Female with face more tumid than in male, clypeus swollen, broadest at middle, sutures distinct, lorae broad and tumid. Last ventral segment a third longer than preceding, margin with sides sinuate and a distinct, small median angulate emargination. A pair of fine brown parallel lines extends medially from sides of this emargination to base of segment.

Color: male tawny with brown eyes, margins of bases of outer spines on hind tibiae, tarsal spines, all claws, and tip of beak; outer and apical portions of elytra with faint suggestion of smokiness; female tinged with bright green anteriorly and below, basal angles of scutellum and anterior impressions of pronotum bright yellow.

Male.—Length, 4.5 mm., width, 1.5 mm. *Female.*—Length, 4.75 mm., width, 1.5 mm.

Male holotype, allotype, taken in Davis Mts., Texas, near Ft. Davis, Aug. 2, 1937, by D. J. and J. N. Knull from *Salix* sp. 15 paratypes from the same locality were taken in June and August, 1937, and September, 1938. All are placed in the collection of The Ohio State University.

TWO NEW FORMS OF HESPERIA

(Lepidoptera, Hesperiidae)

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Although it has been against my idea of useful taxonomic procedure to name subspecific categories, in this genus a few subspecific names seem necessary to call attention to the relations existing in the extremely variable western species. What the subspecific divisions should be called is a matter of opinion. They are generally characteristic of geographic areas in my series, but they crop out far from these centers in small numbers. Until more can be known of the reason for this apparently sporadic occurrence, the noncommittal word *form* seems best to designate them.

One of these forms belongs to the complex so long designated as *Hesperia comma* Linn., including the North American *colorado*, *idaho*, *manitoba*, *assiniboia* and others. The range of variation is extreme and the study of long series of wide distribution indisputably links variants that might easily be taken for distinct species in the absence of intermediate specimens. Two of Edwards' lost species, moreover, prove to belong to this complex. These two, *harpalus* and *cabelus*, are the same as *yosemite* Leussler, more recently described. *Oregonia* Edw. also falls within the range of variation of this form, at the extremity showing maximum development of the spots on the under surface.

It seems doubtful at present that the North American insects are conspecific with European *comma*, hence the species takes the oldest name of the American group—*colorado*.

Hesperia colorado form **leussleri** nov.

Male.—Upper surface closely resembling the majority of the species of this genus, with yellow-fulvous discal areas and fuscous marginal areas enclosing yellow-fulvous spots. The marginal areas are very variable in width and in the distinctness of their inner margins.

Under surface with a pronounced ochreous ground color on the apex of the primaries and entire area of the secondaries. In darker specimens this ground color is definitely darker through the presence of fuscous scales except in the cell and anal area of the secondaries. The usual

bent row of spots and a few basal spots are present on the secondaries, with the anterior spot, between Cu and R, small or lacking. These spots and those on the apex of the primaries are normally whitish, sometimes clear white, and sometimes with a trace of silky luster. The band varies from narrow to moderately wide, but in all cases is conspicuously paler than the ground color. Only rarely does an atypical specimen show less contrast.

Female.—As is usual among these insects, the female differs from the male in having the cell and base of each wing merely suffused with fulvous so that the entire extradiscal row of spots appears isolated against the darker ground. On the secondaries the upper surface shows the extradiscal row of spots and one in the cell faintly in the diffuse fulvous area.

On the under surface the secondaries and apex of the primaries are darker than in the male, showing distinctly gray-brown with scattered ochre scales in darker specimens to a more uniform ochraceous in paler individuals. The spots are well defined, usually rather large and contiguous, and sometimes preceded and followed by dark shades. They show a slight silky luster.

Expanse of the type series: Male, 26 to 30 mm.; female, 30 to 33 mm.

Holotype male and allotype female, Warner's Hot Springs, San Diego Co., Cal., June 13, 1939, to be placed in the Carnegie Museum, Pittsburgh, Pa.

Paratypes as follows: 20 males and 14 females, same lot as above, 2 females, same locality, June 12, 9 males and 4 females, Eagle Peak, San Diego County, Cal., 7 males June 4 and 2 males and all females June 13. Of the foregoing, totalling 49 specimens, 19 males and 14 females are being returned to Captain W. P. Medlar, Research Associate in Lepidoptera, Museum of Natural History, San Diego, Cal., who supplied all of this material for study. The remainder are in the author's collection. 2 male paratypes, Idyllwild, Riverside Co., Cal., 5300 ft., June 29, 1929, and 1 female, July 3 (John S. Garth); 1 male, Big Bear, Cal., 7000 ft., June 21, 1929 (Garth) are in the collection of Mr. R. A. Leussler, Omaha, Neb. 4 males and 2 females, Nellie, San Diego Co., Cal., July 20, 1924, are in the author's collection.

It is a pleasure to name this form for Mr. R. A. Leussler, whose recognition of *pahaska* and *yosemite* has been so helpful in eliminating some of the confusion that has hindered the study of the genus.

Among the names previously established *oregonia* Edw. is nearest to this form; the placing of the name is a matter of interpretation. To me the type of *oregonia* seems definitely to

belong in the better-marked extreme of *harpalus*, with the spots on the under surface scarcely lighter than the ground color, which is of a duller and darker shade than in *leussleri*. I have a few specimens from San Diego County and a few from the Yosemite area that cannot be separated. In short, the gradation between typical *harpalus* of the west slope of the Sierra and typical *leussleri* of the arid lands to the south and east is gradual, and the name *oregonia* applies to borderline specimens.

In the other direction *leussleri* merges with *idaho* Edw. which is typically somewhat grayish-yellow below with a conspicuous macular band of silky white. *Idaho* is abundant in Utah, Nevada and northeastern California, and extends into Oregon, Idaho, Colorado, Wyoming, and the Black Hills of South Dakota (Leussler). It is normally larger than *harpalus* and *leussleri*, though in Wyoming specimens of very small size, otherwise like those of northern California, are to be found. These small specimens link the form with typical *colorado*, which flies at high altitudes. *Colorado* has deep greenish overscaling on the under surface, with a conspicuous white band, sharply bent and usually shortened by the absence of a spot at each end.

Leussleri merges also with a Colorado form that is distinctly ochreous below, with reduced maculation, but there is some confusion in these ochreous Colorado *Hesperia* forms that I cannot at present clear up. In the limited amount of material on hand some specimens seem definitely like *leussleri* while others suggest relationship with *manitoba*. The last may be a related species, rather than a form of *colorado*.

In another of the well-marked species of the genus, *pahaska* Leussler, I find a variant, usually typical of the southwestern states and northern Mexico, that is sufficiently distinct to demand a name. This variant first came to my attention through a series sent by my friend, Captain R. C. Williams, Jr., of Philadelphia, for whom I take pleasure in naming it.

Hesperia pahaska form **williamsi** nov.

Male.—Upper surface quite like the prevailing appearance of the western species. Yellow-fulvous normally less restricted than in typical *pahaska* and tending to invade the fuscous margins as a suffusion. On the under surface the overscaling is normally pale ochreous with a greenish or grayish tinge, and the spots are clear white, reduced in size and tending to be small, rounded, and separate. The separate spots are often outlined with ground color free from ochreous overscaling.

Female.—Much like the male. The tendency to a broad suffusion of yellow-fulvous on the upper surface is more pronounced in this sex, although some specimens are dark, with sharply defined spots. The pale overscaling of the lower surface and the reduction and separation of the white spots are as in the other sex.

Expanse: Male 30–33 mm.; female 32–39 mm.

Holotype and allotype, Baboquivari Mts., Pima Co., Ariz., (O. C. Poling), April 1–15 and Aug. 10, respectively, in the Acad. Nat. Sci., Philadelphia. Paratypes: Four in the collection of Mr. R. A. Leussler, Omaha, Neb., as follows: 1 male, Baboquivari Mts., Pima Co., Ariz., July 1–15, 1924 (O. C. Poling); 1 male and 2 females, Sunny Glen Ranch, near Alpine, Brewster Co., Texas, over 7000 ft., July 17, 1, and 3 respectively (O. C. Poling). Eighteen in the Acad. Nat. Sci. at Philadelphia as follows: Baboquivari Mts., Pima Co., Ariz., (O. C. Poling), 1 male, 2 females, April 1–15, 1923, and 2 males and 3 females, April 15–30, 1923; Arizona, 1883, (H. K. Morrison), 2 males; Carr Canyon, Huachuca Mts., Cochise Co., Ariz., Aug., 1905 (H. Skinner), 1 male; Jemez Springs, Sandoval Co., N. M., (John Woodgate), June 21, 1914, 1 female and June 8, 1922, 1 male; Gila River, Socorro Co., N. M., July 12, 1901, 1 female; Ft. Wingate, N. M., June 3, 1907, 1 male; Alpine, Brewster Co., Tex., 5000 ft., April 7, 1 male and June 19, 1926 (O. C. Poling), 1 female; Double Horn, Burnet Co., Tex., May 25, 1895, 1 female. Four in the author's collection as follows: 2 males collected by Hebard, data lacking; 1 female, Mohave Co., Ariz., Sept. 8–15; 1 female Grand Canyon, Ariz., May 21.

This form was first labelled as a distinct species, based on specimens with small and separate spots on the definitely yellowish undersurface. Genitalic resemblance and a few intermediate specimens led to the proper association with *pahaska* Leussler, and the receipt later on of a series from Mr. W. H. Evans of the Museum of Natural History in London showed that it is not constant as a geographic race. The Museum specimens from the southwestern states were much like typical *pahaska* from more northern localities. A single Mexican specimen in the Museum material belonged to this form.

ARKANSAS CYCLOCEPHALINI WITH NOTES ON BURMEISTER TYPES

(Coleoptera: Scarabaeidae)[1]

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In connection with some biological investigations on *Cyclocephala immaculata* (Oliv.), I have made a study of other Arkansas species within the same tribe. The purpose of this paper is threefold: to present a key for the identification of the males of known Arkansas Cyclocephalini, to record briefly their distribution within the state, and to point out and illustrate certain taxonomic characters that heretofore have received little attention.

Until the many genera and subgenera of Cyclocephalini in North America are better understood, I propose to regard the six Arkansas species as belonging to two genera: Dyscinetus with one species, and Cyclocephala with the remaining five species. Following Saylor's conclusions in his work on California Cyclocephalini (1937), I agree that Casey's Ochrosidia is not sufficiently distinct from the western Spilosota, and the latter may be no more than a subgenus of Cyclocephala. One of our species, *dimidiata* Burm., has been placed by Casey in his genus Dichromina, based primarily upon his assumption that the hind tarsi are shorter than the tibiae. For the present, however, this species will be included in Cyclocephala.

Saylor (1937) figured the male genitalia of all California Cyclocephalini, except *C. dimidiata* Burm. In this paper, figures of the genitalia are presented for all Arkansas species, and in addition, attention is given to the mouthparts. Some of these structures were described in situ by Casey, but apparently no comparative study of the mouthparts of our species has been attempted. While no attempt is made in the descriptive part of

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[1]Research Paper No. 659, Journal Series, University of Arkansas.

Acknowledgments: I am especially grateful to Doctor H. B. Hungerford of the University of Kansas for securing the loan of the Burmeister types of *Cyclocephala villosa*, *nigricollis*, and *dimidiata* for my study. I also appreciate the records and specimens of Arkansas Cyclocephalini secured by Dr. William R. Horsfall, University of Arkansas.

this paper to compare structure for structure, a study of the plates will show the variation from species to species.

Particular attention is called, however, to differences between *C. immaculata* (Oliv.) and *C. borealis* Arrow (*villosa* Burm.), two species of some economic importance in the United States.

CYCLOCEPHALINI

The Arkansas species in this tribe conform to Casey's (1915) diagnosis of the group. The labrum is concealed, and, except in Dyscinetus, is highly sclerotized. Head and thorax without processes; thorax very nearly similar in the two sexes. Stridulating structures absent. Inner claw of anterior tarsus of male enlarged, and in four of our species, bifid. Tarsi usually slender and filiform. Labial palpi 3-segmented, inserted near the sides of the mentum. Mandibles visible from above although occasionally only the tip showing. Hind tibia with two apical spurs.

KEY TO MALES OF ARKANSAS CYCLOCEPHALINI

1. Color piceous or black; middle coxae contiguous; mandibles broad, conspicuously rounded externally.....**Dyscinetus trachypygus**
   Color variable, not entirely black; coxae separated; mandibles narrow, nearly straight externally.....(2)
2. Head and thorax much darker than elytra; clypeus distinctly angulate each side on front margin.....**C. dimidiata**
   Head and thorax very nearly or concolorous with elytra; front margin of clypeus rounded.....(3)
3. Anterior tibia with only one apical tooth developed; larger claw of anterior tarsus of male not bifid.....**C. knobelae**
   Anterior tibia with three well developed teeth; large claw variable.....(4)
4. Thorax above in male very conspicuously clothed with erect hairs; thorax lighter than elytra; larger claw of anterior tarsus of male not bifid..**C. robusta**
   Thorax not clothed with erect hairs; not lighter than elytra; large claw of anterior tarsus of male bifid.....(5)
5. Posterior declivity of elytra of male with long hairs; erect hairs on pygidium fully as long or longer than width of hind tibia at apex; lacinia untoothed, **C. borealis**
   Declivity without hairs or with very short ones; hairs on pygidium shorter than width of hind tibia at apex; lacinia 6-toothed.....**C. immaculata**

Dyscinetus trachypygus (Burm.)

Chalepus trachypygus Burm. Handbuch der Ent. V, 1856, p. 76.
Dyscinetus trachypygus Burm. Casey, Memoirs on the Coleoptera, VI, 1915, p. 171.

This is a common species in the eastern part of the United States, and has been collected in twelve widely distributed counties in Arkansas. It has been collected in the state from Feb. 3 to Oct. 26. Most of the specimens have been taken at light, but upon two occasions were found in mud under chunks of wood around the margins of ponds. The specimen collected Oct. 26 was found about grass roots.

The extremes in size of Arkansas specimens on hand are from 13.5 mm. (a male) to 19 mm. (a female). The color is almost invariably a deep black, but occasional specimens show a greenish tinge. The inner claw of the front tarsus of the male is enlarged, and is normally provided with a small tooth on the outer side. The tooth is often missing, pre-

sumably as a result of abrasion. The female has the sides of the elytra inflated.

In Dyscinetus the mandible is rounded laterally instead of straight as in Cyclocephala. The base is produced laterally, a character which it has in common with *Cyclocephala dimidiata* Burm. This species differs further from other Arkansas Cyclocephalini by possessing a membranous labrum, and the mentum is as long as wide. In the Cyclocephala species, the mentum is much longer than wide, and the labrum is highly scelerotized. In Dyscinetus, the stipes has but two setae arising from the outer margin. The middle coxae are contiguous, a character approached only by *Cyclocephala dimidiata* Burm. The lacinia of *D. trachypygus* Burm. is 6-toothed, a character shared with *C. dimidiata* and *C. immaculata* Oliv. The pygidium of this species is very roughly scabriculate.

Cyclocephala dimidiata Burm.

Cyclocephala dimidiata Burm. Hand. der Ent. V, 1847, p. 57.
Dichromina dimidiata Burm. Casey, Memoirs on the Coleop. VI, 1915, p. 161.
Cyclocephala dimidiata Burm. Saylor, Pomona College Journ. of Ent. & Zool. 29, 1937, p. 70.

A single female of this species was collected at light at Stuttgart, Arkansas, in the summer of 1939 by William R. Horsfall. The species was described from Mexico, and ranges from Panama to Arizona and California. This is the first record of the species from Arkansas.

I have been permitted to examine the female type of this species, and found it to agree with the Arkansas specimen. The figures for the male on Plate II were taken from a specimen collected at Acapulco, Mexico.

This species is readily separated from other Arkansas Cyclocephala by having the thorax much darker than the elytra. The color of the thorax varies from deep red to black. The elytra are testaceous. The clypeus is truncate at apex compared with the rounded clypeus in other Arkansas Cyclocephala. Casey describes the hind tarsus as distinctly shorter than the tibia, but this is true only in the female. The large claw of the front tarsus of the male is forked, with the outer and smaller tooth arising near the middle of claw. In other Arkansas Cyclocephala the outer tooth is absent or arises as a very small, slender tooth very near the apex. The lacinia is 6-toothed, which is also characteristic of *Cyclocephala immaculata* Oliv. and *Dyscinetus trachypygus* Burm. The outer margin of the mandible is nearly straight, and with the apex truncate and slightly produced laterally. The lateral margin of the mandible at base is strongly produced as in Dyscinetus. The middle coxae are very narrowly separated.

Other significant characteristics of this species concern the hind tibia and tarsus. The tarsus is comparatively shorter than in other Cyclocephala. There are 7 or 8 coarse spines between the small spur of the hind tibia and the opposite side of the tibia. In other Cyclocephala, the coarse spines are replaced by 12 to 15 slender spinules. In the female of *dimidiata*, the first hind tarsal segment is twice the width of the second and nearly twice the width in the male. In other species, the first two tarsal segments are subequal in width.

Cyclocephala knobelae (Brown)

Ochrosidia knobelae Brown, Can. Ent. LXVI, 1934, pp. 23–24.

Through the courtesy of Mr. George A. Moore of McGill University, Montreal, Canada, I have been permitted to examine a paratype male of this species. The type series, consisting of two males and two females, was collected at Hope, Arkansas, and was not accompanied with additional information. This species, the smallest known from Arkansas, has the entire dorsum, except a nearly impunctate area on vertex of head and clypeus, clothed with fine, sparse hairs. It may be readily separated from other Arkansas species by its small size (the paratype male measured 9 mm. in length), and the possession of a single tooth on the anterior tibia. Other species have the usual three teeth. The large claw of the anterior tarsus of the male is not bifid, a character agreeing with *robusta* Lec. The single antenna in the paratype is, apparently, only 8-segmented. Other species in our fauna have 10 segments.

Cyclocephala robusta Lec.

Cyclocephala robusta Lec. Smith. Misc. Coll. VI, 1866, p. 79.
Cyclocephala nigricollis Burm. Hand. der Ent. V, 1847, p. 54.
Cyclocephala nigricollis Burm. Horn, Trans. Amer. Ent. Soc. III, 1871, p. 336.
Cyclocephala nigricollis Burm. Buchanan, Ent. News, 38, 1927, p. 167.
Ochrosidia subvittata Brown, Can. Ent. 62, 1930, p. 5.

Considerable confusion has existed in the correct identification of this species. Horn (1871) considered *robusta* Lec. a synonym of *nigricollis* Burm. based upon his examination of types of both species. Buchanan (1927) also regarded *robusta* Lec. as a synonym of *nigricollis* but based the synonomy upon Horn's statement. He described and figured the sexes, and recorded the species as occurring in Louisiana. Through the courtesy of Doctor W. Ludwig of the Zoologisches Institut, Halle, Germany, I have been permitted to examine the female type of *nigricollis*, in addition to other Cyclocephala mentioned elsewhere in this paper, and consider *nigricollis* as distinct from females of *robusta*. It differs from robusta as follows: the front angles of the thorax are strongly angulate and pointed in *nigricollis* compared with the rounded angles in *robusta*. In *nigricollis*, the margin of the elytra is rather suddenly widened and enlarged near the middle and interrupted by an indentation behind the enlargement. The elytral margin in *robusta* shows no evidence of enlargement at any point. In the type female of *nigricollis*, the large spur of the hind tibia is about three times longer than wide, while the length of the same spur in the female of *robusta* is less than twice its width. In *nigricollis* the middle tooth of the front

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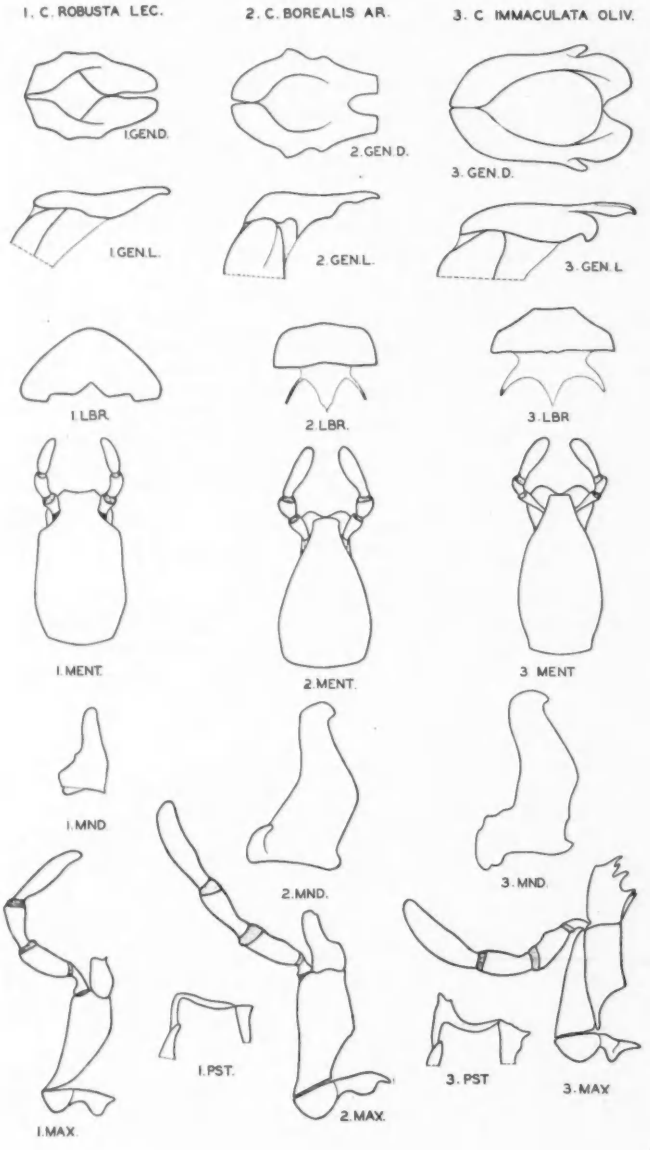
EXPLANATION OF PLATE I

Fig. 1. *Cyclocephala robusta* Lec.
Fig. 2. *Cyclocephala borealis* Arrow.
Fig. 3. *Cyclocephala immaculata* (Oliv.).

Gen. d.—genitalia, dorsal view. Gen. l.—genitalia, lateral view. Lbr.—labrum, ventral view. Ment.—mentum, ventral view. Mnd.—right mandible, dorsal view. Max.—left maxilla. Pst.—prosternum, lateral view.


1. C. ROBUSTA LEC.
2. C. BOREALIS AR.
3. C IMMACULATA OLIV.
1.GEN.D.
2.GEN.D.
3. GEN.D.
1.GEN.L.
2.GEN.L.
3. GEN.L
1.LBR.
2.LBR.
3.LBR
1.MENT.
2.MENT.
3 MENT
1.MND.
2.MND.
3.MND.
1.PST.
2.MAX.
3.PST
3.MAX
1.MAX.

tibia is closer to the anterior tooth than to the posterior. In *robusta*, the middle tooth is separated equally from the other teeth.

Mr. W. J. Brown (1930) very kindly sent me a paratype male of *C. subvittata* Brown for study, and it is here regarded as a synononym of *robusta* Lec. *C. robusta* is variable in coloration, and his species represented the lighter colored specimens. The genitalia of the paratype of *subvittata* and specimens of *robusta* were the same.

C. robusta has been taken very commonly in light traps at Stuttgart, Arkansas. Males only were secured. In the males, the thorax and elytra are clothed with long, erect hairs. The thorax is lighter than the elytra and in some specimens has a light longitudinal line from base to apex on either side of which there is a darker area. The female of this species is glabrous above.

This species is related only to *C. knobelae* Br. among the Arkansas species, although differing in several respects. The males agree in the possession of long hairs on the thorax and elytra, and the uncleft large claw of the anterior tarsus, by which characters they may be distinguished from other Arkansas species of this genus. The lacinia of *C. robusta* Lec. has a single small tooth arising near the apex. The mandible is narrow with the outer margin straight. In this species, the prosternum between the front coxae is nearly straight when viewed laterally. In *C. immaculata* Oliv. and *C. borealis* Arrow, the prosternum is deeply emarginate.

Cyclocephala borealis Arrow

Cyclocephala villosa Burm. Hand. der Ent. V, 1847, p. 54.
Cyclocephala villosa Burm. Casey, Mem. on Coleop. VI, 1915, p. 147.
Cyclocephala borealis Arrow, Ann. Natl. Hist., 8th series, vol. 8, 1911, p. 172.

Although this is a widely distributed and abundant species in the eastern United States, in Arkansas it has been collected thus far only at Stuttgart. In June several specimens were collected by Dr. William R. Horsfall in a trap light, and they appeared to be most abundant between 1:30 and 3:30 in the morning. Males only were collected. The Arkansas specimens that have been examined are nearly as light in color as *immaculata* Oliv. and average nearly the same in size. Specimens of *borealis* Arrow from Ohio and other eastern states appear to be somewhat darker and in this respect agree with the types which I have been permitted to examine. In structural detail, however, the lighter and darker specimens appear to be the same.

In the Arkansas fauna, *borealis* is closely related only to *immaculata* and in most specimens is readily distinguished by the long hairs on the

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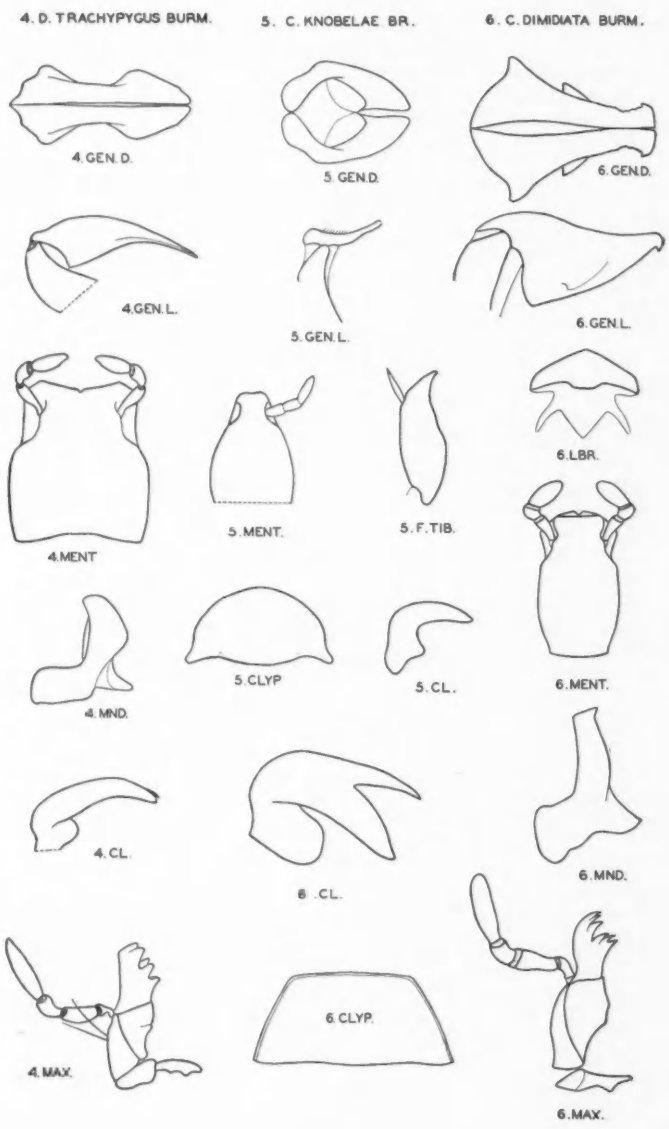
EXPLANATION OF PLATE II

Fig. 4. *Dyscinetus trachypygus* (Burm.).
Fig. 5. *Cyclocephala knobelae* (Brown).
Fig. 6. *Cyclocephala dimidiata* Burm.

Gen. d.—genitalia, dorsal view. Gen. l.—genitalia, lateral view. Lbr.—labrum, ventral view. Ment.—mentum, ventral view. F. tib.—fore tibia. Mnd.—right mandible, dorsal view. Clyp.—clypeus. Cl.—front tarsal claw of male. Max.—left maxilla.


4. D. TRACHYPYGUS BURM.
5. C. KNOBELAE BR.
6. C. DIMIDIATA BURM.
4. GEN. D.
5. GEN. D.
6. GEN. D.
4. GEN. L.
5. GEN. L.
6. GEN. L.
6. LBR.
4. MENT.
5. MENT.
5. F. TIB.
6. MENT.
4. MND.
5. CLYP.
5. CL.
4. CL.
6. CL.
6. MND.
4. MAX.
6. CLYP.
6. MAX.

elytral declivity, elytral margins, and pygidium. The pygidial hairs of *borealis* are fully as long as or longer than the width of the hind tibia at apex. It is further distinguished from *immaculata* by its untoothed lacinia, the absence of curved processes on the parameres of the genitalia, and by differences in the mouthparts as demonstrated in Plate I.

The name *borealis* Arrow replaces *villosa* Burm., the latter having been used previously by Blanchard for a Bolivian species.

Cyclocephala immaculata (Oliv.)

Melolontha immaculata Oliv. Entomologie, Paris, 1790, p. 29.
Ochrosidia immaculata Oliv. Casey, Mem. on Coleop. VI, 1915, p. 146.
Cyclocephala immaculata Oliv. Saylor, Pomona College Journ. of Ent. and Zool. **29**, 1937, p. 70.

This is the most widely distributed and apparently the common species of Cyclocephala in Arkansas. It has been collected from April to September, nearly all specimens having been taken at light. The males almost invariably predominate in these collections. The average size is about 13 mm.

Among the Arkansas species, this is closely related only to *C. borealis* Arrow. In recently transformed adults, there may be a few scattered very short hairs on the posterior half of the elytra. The erect hairs on the pygidium are conspicuous but not as long as the width of the hind tibia at apex. In *borealis*, the pygidial hairs are fully as long or longer than tibia at apex, and in most specimens the hairs on the posterior elytral declivity are arranged in rows, and are long and conspicuous. The male genitalia of *immaculata* has a prominent process on the outer side of each paramere, while there are no processes in *borealis*. The lacinia of *immaculata* has six teeth although the middle one at base is often very small. The lacinia is without teeth in *borealis*. Other differences may be noted in the maxilla, mandibles, mentum, and labrum by reference to Plate I.

THE WASMANN COLLECTOR

The ANNALS wishes to call to the attention of members of the society, the recently established journal, *The Wasmann Collector*, which will carry among articles on various biological subjects certain articles in the pure science of entomology.

The Wasmann Collector was established as the journal of the Wasmann Biological Society formed by students and alumni of the University of San Francisco, a Jesuit institution. On the union of the Pre-Medical Society of Loyola University of Los Angeles with the Wasmann Society as a chapter of the San Francisco organization, it was decided to establish a chain of such science societies at other American Jesuit colleges and universities. *The Wasmann Collector* will be the journal for all and will be edited and published at the University of San Francisco. It was named for the Jesuit, Father Erich Wasmann, who wrote endlessly on the psychology of ants. He was the last of the great apostles of teleology. He was *anti* all mechanistic explanations of the habits of ants, termites, etc. He worked particularly on the involved relationships of ants and myrmecophiles.

The April, 1940, issue is No. 1 of Vol. 4. It carries among other articles one by A. N. Bragg of the University of Oklahoma on the ecology of Anura, and a twelve-page article by M. A. Cazier of the University of California on "New North American Achmaeodera" which are Buprestids.—C. H. K.

THE GROWTH OF THE HEAD CAPSULE OF THE JAPANESE BEETLE LARVA

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The fact that the width of the head capsule of an insect larva is more or less constant for any instar of a species was first demonstrated by Dyar (1890) in his study of lepidopterous larva. This characterization of an instar by head measurements has recently been extended to a large number of species belonging to many orders of insects. The Japanese beetle passes through three instars in its larval development. In the present paper, an analysis is made of a large number of measurements of both the width and the length of the head capsule of the larva at different stages of development to determine if these measurements are characteristic of each instar and can be used to separate random samples of larvae into the three instars. This separation is possible only if there is no overlapping of measurements made on larvae of successive instars.

Dyar (1890) observed that the width of the head of lepidopterous larvae follows a regular geometric progression in successive stages. According to this rule, it should be possible to determine the width of the head capsule at any stage from the equation $\log y = a + bx$ (Forbes, 1934; Gaines and Campbell, 1935). In this equation y is the width of the head, x is the number of the instar, a is a constant, and b is the logarithm of the growth ratio or the progression factor. However, Gaines and Campbell, in their work on the corn ear worm, *Heliothis obsoleta*, obtained growth ratios which were high in the early stages and which progressively decreased during growth. They showed that, because of this trend in growth ratios, the relationship between head width and the stage of development could more accurately be described by the second degree equation $\log y = a + bx + cx^2$, where y and x have the same meaning as in the former equation, and a, b, and c, are constants.

Abercrombie (1936), in his study of cell number and the progression factor in the growth of the Japanese beetle, found that the ratio of head length of the second instar larva to that of the first instar larva was 1.89; and of the third instar to that of the second instar, 1.65. Corresponding ratios for head width were 1.63 and 1.58. Hence, in this insect there is also a decrease in growth ratios with age. These ratios for the length and width of the head capsule are different although both describe linear growth. They suggest that disharmonic or heterogonic growth of the head may occur during larval development. The relationship which exists between parts of an organism which show heterogonic growth is expressed by the equation $y = bx^k$, where y is the magnitude of the differentially growing organ, x is the magnitude of the animal or of some part of the animal to which the organ is compared, b is a constant, and k is the differential growth ratio (Teissier, 1931; Huxley, 1932). If k is equal to one, growth is isogonic; whereas, if it is greater or less than one, growth is heterogonic.

The present analysis of the head measurements of the Japanese beetle larva includes a comparison of the applicability of the formula for the regular geometric progression and the second degree equation, as well as a study of the relationship which exists between the increase in length and width of the head capsule during larval development. The measurements made by Abercrombie (1936) together with others made by the senior author are studied in this paper. The procedure outlined by Abercrombie (pp. 94–95) was also employed by the senior author.

OBSERVATIONS

The frequency distributions for the length and width of the head capsule of Japanese beetle larvae are plotted in Figure 1. In each case there are three well defined groups of measurements corresponding to the three larval instars. Moreover, the measurements for each instar are separate and distinct, the smallest individual of an instar being distinctly larger than the largest individual of the preceding instar. Therefore, it is possible, on the basis of head measurements alone, to assign each individual of a random collection of larvae to its proper instar. As a test of this conclusion, two groups of third instar larvae were selected for measurement. One group contained 18 newly molted larvae reared in a medium which produced exceptionally small individuals, while the other group contained 12 full-grown larvae reared in media which produced large individuals. The average weight of the first group was 50.3 milligrams, and of the second group, 313.3 milligrams. In spite of this difference in weight between the two groups, all measurements of

head size fell within the limits of this stage plotted in Figure 1, with the exception that several measurements of 3.4 millimeters were obtained for head width, whereas the highest value plotted in the figure was 3.35 millimeters. Hence, it seems very unlikely that any measurement of head size made on larvae obtained in the field would fall outside the limits for each instar as found under laboratory conditions and plotted in Figure 1.

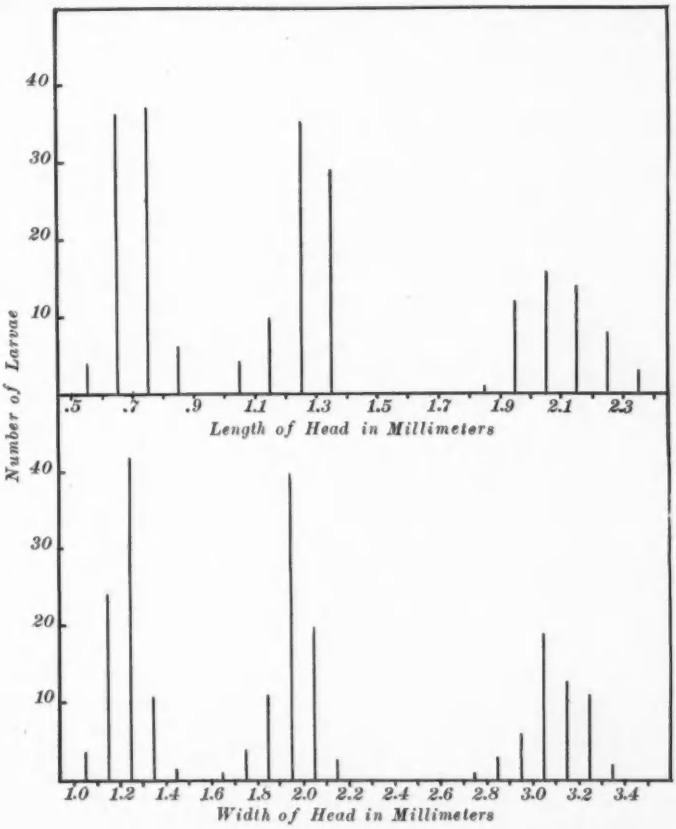

Figure 1. Frequency distributions for the length and width of the head capsule of Japanese beetle larvae.

Growth ratios, describing the increase in length and width of the head capsule in successive instars were obtained from the formula log $y=a+bx$. The values of the constants a and b were calculated by the method of least squares. The equation for determining the length of the the head was found to be log $y=0.2376\ x—0.390$; and for the width of

the head, it was log y=0.2035 x—0.122. These formulae gave ratios of 1.73 for length and 1.60 for width (reciprocal of Dyar's ratios). The mean observed head measurements are compared with the values calculated by each of these formulae in Table I. Second degree parabolic equations of the form $\log y = a + bx + cx^2$, for the growth in length and width of the head capsule, calculated by the method of least squares, together with the values obtained from these equations are also given in the table. If the increase in size of the head capsule follows a regular geometric progression, as postulated by Dyar (1890) for lepidopterous larvae, then the relationship should be expressed more accurately by the

TABLE I

COMPARISON OF OBSERVED AND CALCULATED VALUES (IN MILLIMETERS) OF MEAN MEASUREMENTS OF THE HEAD CAPSULE OF JAPANESE BEETLE LARVAE

NUMBER OF INSTAR	I	II	III
LENGTH OF HEAD CAPSULE			
Observed length	0.695 ± 0.0052	1.247 ± 0.0064	2.076 ± 0.011
Calculated length (Log y=0.2376x—0.390	0.704	1.216	2.102
Difference	0.009	0.031	0.026
Calculated length (Log y=0.298x—0.015x²—0.441)	0.695	1.245	2.080
Difference	.....	0.002	0.004
WIDTH OF HEAD CAPSULE			
Observed width	1.201 ± 0.0061	1.945 ± 0.007	3.066 ± 0.012
Calculated width (Log y=0.2035x—0.122)	1.206	1.928	3.080
Difference	0.005	0.017	0.014
Calculated width (Log y=0.228x—0.006x²—0.143)	1.200	1.946	3.069
Difference	0.001	0.001	0.003

straight line equation. However, if the observed values agree more closely with those obtained by the use of the second degree equation, the relationship is not a regular geometric progression, but when the logarithms of the head measurements are plotted against the number of the instar, a curved line should result. A comparison of the observed values with those calculated by each method shows that for both length and width measurements, the second degree equation gave values which more closely agree with those observed. Hence, the increase in the size of the head of the Japanese beetle larva in successive instars does not appear to follow a regular geometric progression. Deviations from the straight line relationship would be more evident in an insect which passes through many molts in its larval development.

In figure 2 the increase in width of the head capsule is plotted against its increase in length. This relationship is a straight line of the equation

$y = 1.35\,x + 0.263$, where y is the width of the head capsule, and x is its length. Although the ratio for the increase in width of the head in successive instars is not the same as the ratio for its increase in length, the increase in width is directly proportional to the increase in length. Hence, proportionate or isogonic growth of the head occurs during larval development.

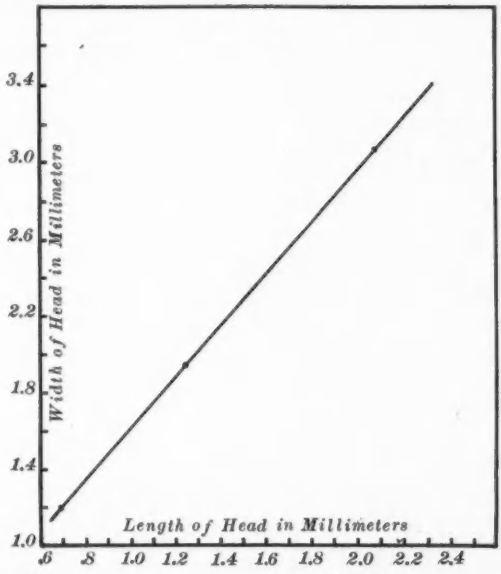

Figure 2. Relationship between the increase in width and the increase in length of the head capsule of the Japanese beetle larva in successive instars. The straight line is the graph of the equation $y = 1.35x + 0.263$. Points represent the observed head measurements at each instar.

DISCUSSION

The complete separation of all measurements of the head capsule into three distinct groups is probably associated with the fact that since there are only three larval instars in the Japanese beetle, the size differences between successive instars must be quite large. The average growth ratios of 1.73 and 1.60 reported in this paper are larger than those obtained for linear growth by most workers, (Harries and Henderson 1938, Table II), or the ratio 1.26 found by Przibram and Megusar (1912) for the Egyptian praying mantis, *Sphodromantis bioculata*, and applied to linear growth of many other insects by Bodenheimer (1927). For holometabolous insects, Bodenheimer believed that the increase in length of any part could be better expressed by some exponent of 1.26, such as $(1.26)^2$ or 1.59, indicating the presence of latent molts. However, Abercrombie (1936) showed the inapplicability of this interpretation to the growth of the Japanese beetle. Furthermore, Harries and Hender-

son (1938) in their review of insect growth rates, concluded that "the variation shown in the value of the progression factor is too great to provide any support for the theory that the constant has the same value (1.26) for different species." They showed also that there is no grouping of progression factors around the value 1.59 as one would expect if Bodenheimer's hypothesis were correct.

The progressive decrease in the growth ratios with successive stages in the larval development of the Japanese beetle, described in this paper and also by Abercrombie (1936), agrees with the observations of many other investigators on many different groups of insects. Gaines and Campbell (1935) studied more than 800 growth ratios obtained for lepidopterous larvae by various investigators and found that there is a definite tendency for these ratios to diminish with age. This regular decrease in growth ratios renders the use of an average ratio for the entire growth period of rather questionable value.

SUMMARY

1. The length and width of the head capsule of Japanese beetle larvae were measured at different stages of development. These measurements fall into three well defined groups, each characteristic of a larval instar. Hence, they can be used to assign each individual of a random collection of larvae to its proper instar.

2. The growth ratios for both length and width of the head capsule diminish with successive stages. Hence, the growth of the head can be more accurately described by the parabolic equation of the form $\log y = a + bx + cx^2$ than by the straight line equation $\log y = a + bx$.

3. Although the ratios for the increase in head length are different from those for increase in head width, the increase in the length of the head is directly proportional to its increase in width.

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RELATIVE PREVALENCE OF POTATO FLEA BEETLE INJURIES IN FIELDS ADJOINING UNCULTIVATED AREAS

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Ecological effects on potato fields adjoining uncultivated areas were observed in western New York State in 1931, 1932, and 1933.[1] Although general observations were made in many fields of potatoes, data were obtained in 1933 from a number of specific fields on the muck soils of Orleans and Genesee Counties.

Measurements of the effects were made by examining potato tubers for injuries made by larvae of the potato flea beetle (*Epitrix cucumeris* (Harr.)). Lots of 100 tubers were dug, brushed, and examined to serve as samples for each point under observation. One large potato tuber was selected from each lot for a qualitative determination of injuries sustained. Selection of the large tuber was made by picking the most convenient one at hand.

TABLE I

INFLUENCE OF UNCULTIVATED AREA ON NUMBERS OF INJURIES TO TUBERS BY LARVAE OF THE POTATO FLEA BEETLE

Distance from Uncultivated Area (in feet)	Number of Tubers per 100 Showing Injuries	Number of Injuries per Selected Tuber
0	18	3
100	12	3
200	6	2
300	9	0
400	5	0
500	6	0

Of the fields examined, one field which exhibited the most obvious effects was a large one (10 to 12 acres), bounded on its western end by uncultivated land of uncleared trees and underbrush. Cultivated areas that joined the two sides and the eastern end precluded influence from adjoining uncultivated areas. The variety was Bliss Triumph. Lots of 100 tubers were dug at the western end of the field and at intervals of 100 feet from the end. The data obtained are presented in Table I.

These data indicate (1) that, qualitatively and quantitatively, the tuber injuries were measurably related; (2) that there were more tuber

[1]Acknowledgments are made to Dr. G. F. MacLeod for his suggestions, interest, and other assistance in this work.

injuries near uncultivated areas than at greater distances inside the field; and (3) that there appeared to be a decrease in the number of injuries to a distance of more than 100 feet, then a tendency to an equalization of injuries as distance into the field increased.

In another field of potatoes, of the Cobbler variety, the west end and south side of which adjoined woodlands, there were more injuries in the west and south portions than in the north and east portions, which adjoined cultivated areas. A heavy undergrowth of the usual muckland plant societies of small trees, shrubs, and other plants covered the ground; plants of the perennial blue nightshade (*Solanum dulcamara* L.) were especially abundant on the west and south side of the field. Data in substantiation of this are presented in an ecotopographic map (fig. 1, after Hartzell).[2] Lines of equal injuries, larval isofags, are shown in relation to the phytic environment. Lines of equal elevation, isohyps, were not drawn because the area was practically level.

The field was sampled by digging lots of 100 tubers from sections of rows at given distances from the sides and ends. Each tuber was brushed and examined for injuries. The numbers were plotted in their respective locations on a map. Isofag lines were drawn connecting equal numbers of injuries and are shown in figure 1. Statistical treatment gave 35.5 as the mean number of injured tubers per lot of 100 and 11.4 as the standard error.

Data were also recorded for the number of larval injuries, at each sample point, per tuber of 3-inch diameter size. Although no figure is shown for these observations, curves of exactly the same form and type were obtained as are shown in figure 1.

The influence of uncultivated areas from two directions is observed in figure 1. Overlapping effects are seen along the diagonal, if a line be drawn in a northeast-southwest direction across the potato field. The decrease in rate of injury with increase in distance from uncultivated areas indicates environmental effects of essentially the same magnitude as shown in table I.

In order to determine whether beetles emerged from hibernation quarters in the cultivated soil of a potato field or from the soil of uncultivated areas adjoining the field, samples of soil were placed in cages to collect emerging beetles. Samples of soil which measured 6 by 6 inches on the surface and 4 inches in depth were taken from various places in a potato field. Other samples were taken from various places of untilled areas, such as fence rows, drainage ditch banks, and shrub-covered soil near the field. These samples were collected in the early part of May, before the beetles began to emerge from hibernation. An average of 1.08 beetles emerged from 12 samples of untilled soil, and an average of 0.13 beetle from eight samples of soil from a potato field. The difference is 0.95, which, compared with its standard error, 0.21, is considered significant. Simple computation therefore gives the number of beetles per acre that were hibernating in uncultivated soil as over 188,000, and in the cultivated soil over 22,000.

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[2]Hartzell, F. Z. Ecotopographic maps: their use in entomology and notes on making. Jour. Econ. Ent. 24: 151–157. 1931.

Field observations showed that beetles were less prevalent on plants where large trees cast dense shade. Plants of the blue nightshade do not appear to grow well in such shaded places. These two factors, separately or combined, apparently created an unfavorable environment for the flea beetles, and these conditions were reflected in a comparatively low degree of flea beetle injury to potato tubers in some fields that were studied. Those fields bordering uncultivated areas which were covered by shrubs, small or young trees, and other low-growing plants were the ones which presented the most striking gradations of injuries, as shown. Neither compass direction nor prevailing wind direction was observed to have any influence on the distribution of injuries in the potato fields.

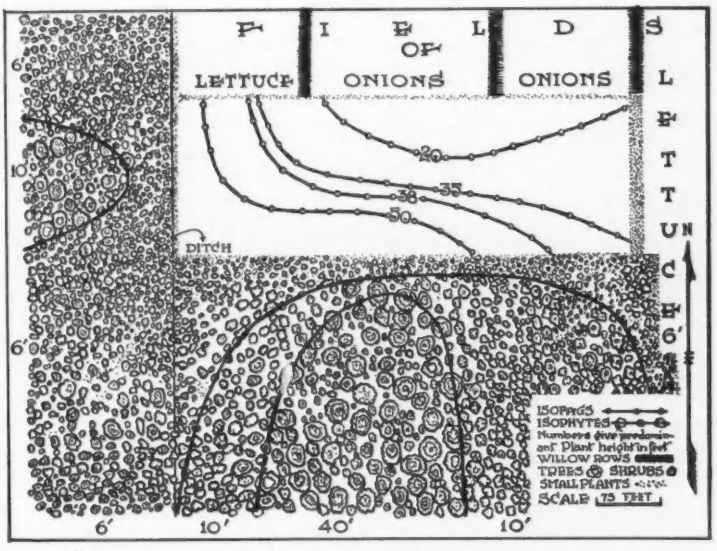

Figure 1.—An ecotopographic map of a potato field and adjacent land.

The data presented indicate that there was some migration of beetles into fields from adjoining uncultivated areas and that at distances of more than 100 feet the effects of migratory beetle dispersion are much reduced. Beetle injuries were always found throughout the fields to a variable degree. Because of (1) beetle hibernation in the fields and (2) beetle dispersion from the uncultivated areas adjoining potato fields, no places where no injuries occurred were observed at any distance, of practical significance, from uncultivated land. A substantial degree of protection from potato flea beetle injuries may be attained, however, by planting potatoes, whenever practical, at a distance of at least 100 feet from favorable field-border vegetation.

The effect of adjoining uncultivated areas in inducing favorable environmental conditions for flea beetles is attributable to the beetles' feeding for a longer period than is represented by the growing period of the potatoes. This lack of synchronization between the seasonal activity of the insects and the host plant compels the insects to feed and to breed, perhaps with less favor, on plants other than the potato. This in turn contributes to the numerical increase in the populations of the insect in the fields bordering areas possessing favorable characteristics. Part of the beetle population goes into hibernation with the death of the potato plants, and part moves to plants on uncultivated soil surrounding the fields, where the beetles feed for a time until they go to the soil beneath for hibernation.

THE LITTORAL FAUNA OF GREAT BRITAIN, A HANDBOOK FOR COLLECTORS, by N. B. EALES. 1939. Pages xvii and 300, 24 plates. Size 5½ x 9 inches. Published by the CAMBRIDGE UNIVERSITY PRESS, Bentley House, N. W. 1, London, and THE MACMILLAN CO., 60 Fifth Ave., New York City. Price $3.50.

Civilized man lives in an environment which differs from that experienced by all other animals. He plunges almost from birth into a world of objects with labels. His first nursery-school text shows a cat, a dog or other object underneath each of which is its printed name. Eventually he learns that language is a system of vocal labels or written labels which can be juggled into sentences, paragraphs and even into written book notices. He soon realizes that life can become very embarrassing if he forgets and mixes labels, and refers to a girl friend as a lemon. He lives in a world of labels. He soon thinks labels.

Curiously enough he tends to avoid objects whose names or labels are unknown to him. Unnamed objects confuse his thinking, or actually make certain types of thought (word juggling) difficult or even impossible.

Hence the pleasure one derives from such a volume as the one before us. Miss Eales, Lecturer in the Zoology Department of the University of Reading, has given us just such a label-fixing work. It keys out and puts names, at least down to genera, on the fauna of the between-tide zone of the shores of the British Isles. As she states herself: "Its object is three-fold: (1) To encourage observation of the habitat, habits and structure of the living animal, (2) To supplement with a closer observation in the laboratory, and (3) To provide a preliminary training in systematic work.

British land life is very meager because of the recent glaciation and the difficulty of spread from the south across the North Sea and the Channel and over mountain ranges that fringe the Mediterranean basin. The littoral fauna appears to have been less disturbed perhaps because of its association with the warm Gulf Stream and its direct connections with more southern continental shores. It is a fairly rich life. Comparative anatomy and systematic zoology started their modern development on these very shores. It was this fauna which enthused Cuvier when, as a tutor in the family of the Compte d'Héricy during the French revolution, he lived with that family at Fécamp near Havre on the Channel. His spare hours were spent collecting and dissecting these curious animals. The great English students of the invertebrates were trained on this same fauna.

The material is handled in thirteen Phyla. This conservative taxonomy is carried throughout the book. Thus the ninety per cent of common animals are named to species while the accidentals, local and rarer forms are not given specific treatment. Each phylum section opens with a short bibliography of monographic works on that group. Keys are moderately simple and anatomical terms are taken care of by numerous labels on the many plates of simple line drawings.

The volume gives the student a balanced picture of a North Atlantic seashore fauna. It is satisfying in this matter of putting labels on objects which usually are without names to even the seashore student of zoology. It is well done and by an experienced student of shore life.—C. H. K.

THE GENUS SYMPYCNUS IN UTAH

(Dolichopodidae: Diptera)[1]

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The seven species of *Sympycnus* here described as new might be placed in the subgenus *Calyxochaetus* Bigot (=*Nothosympycnus* Wheeler). Males of this subgenus differ from typical *Sympycnus* in having the first joint of the fore tarsi greatly shortened and usually having the antennal arista enlarged at tip or with a conspicuous lamella.

The writers have not used subgeneric names in this report due to the fact that some males have the first and second joints of the fore tarsi shortened and of equal length, as in the case in *S. insolitus* Van Duzee; moreover, several males possessing a very short first joint of fore tarsi have a plain antennal arista, lacking a thickened area or a lamella. In most instances the females, unless associated with the males, cannot be definitely placed in the correct so-called subgenus.

A careful study of all Utah *Sympycnus* material in the Utah Agricultural Experiment Station collection indicated that the following corrections should be made in the preliminary list (Utah Agr. Expt. Sta. Min. series 200, Tech., pt. 5: 21) of species: *S. cilifemoratus* V. D. should be *fuscitibialis* n. sp.; *clavicornis* V. D. and *oreas* Wheeler should be *isoaristus* n. sp.; *nodatus* Loew should be *hardyi* n. sp. All species listed in the following key have been collected in Utah by the writers except *S. latitarsis* V. D.; however, this species was described originally from a specimen taken at Wendover, Utah.

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[1]Contribution from the Department of Entomology, Utah Agricultural Experiment Station.

[2]Research assistant and research associate professor, respectively.

KEY TO MALES OF UTAH SYMPYCNUS

1. First two joints of fore tarsi of equal length 2
   First joint of fore tarsi not more than one-half the length of second joint 3
   First joint of fore tarsi at least one and one-third times the length of second joint 9
2. Antennal arista thickened at tip: lower edge of hind femora with three long slender black bristles near apex; third and fourth joints of fore tarsi with dense fringe of hair on upper surfaces ..... **insolitus** Van Duzee
   Antennal arista sharply pointed at tip; posterior femora without bristles on lower edge; fore tarsi plain ..... **tripilus** Van Duzee
3. Front tibiae distinctly swollen 4
   Front tibiae not swollen 5
4. Antennal arista with conspicuous lamella at tip; abdomen yellow on sides of second, third and fourth segments ..... **vegetus** Wheeler
   Antennal arista pointed at tip; abdomen wholly metallic black (p. 398), **spatulatus** n. sp.
5. Antennal arista enlarged at tip, or with a conspicuous lamella 6
   Arista of equal thickness throughout, or sharply pointed at tip 8
6. Arista with a lamella in the middle and another at apex. (p. 397), **binodatus** n. sp.
   Arista with lamella at tip only 7
7. Lamella of arista large, broad; fore femora black on basal half, apical half of hind femora with long cilia on lower edge (p. 400) ..... **fuscitibialis** n. sp.
   Lamella of arista small, yet conspicuous; posterior femora without long hairs or bristles on lower edge (p. 397) ..... **hardyi** n. sp.
   Arista gradually enlarged on apical fifth, feather-like; apical half of posterior femora with long hair-like bristles below; fore femora wholly yellow, **distortus** Van Duzee
8. Arista of antenna very long, pubescent, of equal thickness throughout; base of middle and hind femora each with long cilia on lower edge (p. 399), **pennarista** n. sp.
   Arista long, of equal thickness throughout; femora without bristles or cilia below; apical third of hind femora with three or four long hairs on lower edge (p. 402) ..... **isoaristus** n. sp.
   Arista tapering, sharply pointed at tip; femora without hairs or bristles on lower edge (p. 401) ..... **pictipes** n. sp.
9. Antennae wholly black 11
   First joint of antennae yellow 10
10. Hind tibiae entirely yellow; hind basitarsus narrowly black at tip; last two joints of middle tarsi black, flattened ..... **pugil** Wheeler
    Hind tibiae thickened and black at tip; hind basitarsus white on basal half, black on apical half ..... **clavatus** Van Duzee
11. Legs and body wholly black ..... **utahensis** H. & K.
    Fore femora black on basal half, at least on upper edge 12
    Fore femora wholly yellow 13
12. Front coxae wholly black; hind femora and tibiae wholly yellow, **calcaratus** Van Duzee
    Front coxae yellowish to nearly brown; fore tarsi flattened dorso-ventrally, the second joint with three strong, sharp bristles below. **latitarsus** Van Duzee
    Front coxae yellowish, darkened at base; hind femora and tibiae blackened on apical fourth ..... **cuprinus** Wheeler
13. Front coxae brownish at base; posterior tarsi plain, without bristles, the basitarsus yellow ..... **breviventris** Van Duzee
    Front coxae yellow 14
14. Hind tibiae wholly yellow; third joint of hind tarsi with a large, curved bristle and a few hairs on inner side near the middle ..... **marcidus** Wheeler
    Hind tibiae black, except narrowly at base; abdomen and dorsum of thorax metallic green ..... **canadensis** Van Duzee

Sympycnus binodatus n. sp.

Male.—Length, 2.6 mm.; of wing, 2.8 mm. Face very narrow, the eyes nearly meeting, silvery white; front blue-green, metallic, lightly pollinose immediately above antennae; antennae (fig. 7) black, first joint short, third joint large, nearly as broad as long, its tip broadly rounded; arista very long, with two lamellae, one near middle, the other at tip; orbital cilia brownish above, pale and delicate below.

Thorax dark green, the dorsum and scutellum dusted with brownish-yellow pollen; pleurae greenish, with light greyish pollen; abdomen with first, fourth, fifth and sixth segments metallic black, the second and third segments yellowish except for a narrow dorsal line; hypopygium black, the outer lamellae yellow, tiny, the inner lamellae black, somewhat conical yet with tips rounded.

Coxae, femora and tibiae yellow; fore coxae with pale hairs on their anterior surface, the bristles at tip yellow; middle coxae darkened on outer surface, at base nearly concolorous with pleaurae; fore femora plain, slightly swollen at the base; middle femora with a row of delicate yellowish hairs below, these hairs of increasing length, begin near base and end near middle of femora; middle femora with one preapical bristle, hind femora with two preapical bristles, one located above the other; middle tibiae (fig. 3) with yellowish cilia along entire lower, outer edge; hind tibiae (fig. 2) with a clump of three to five long cilia at base on lower surface; tarsi blackened from tip of first joint; joints of fore tarsi as 2–10–5–3–3; of middle tarsi (fig. 3) as 10–5–1–2–3; of hind tarsi as 8–10–5–4–3. Halteres pale yellow; calypters yellow with narrow brown apical margin, their cilia long, yellowish.

Wings (fig. 1), grayish hyaline; fourth vein ending in wing tip.

Described from one male taken at Leeds, Utah, September 13, 1939, by G. F. Knowlton and F. C. Harmston.

Taxonomy.—This is the only species of North American *Sympycnus* known to the writers which has two lamellae on the antennal arista.

Sympycnus hardyi n. sp.

Male.—Length, 2.2 mm.; of wing, 2.1 mm. Face wide for a male, silvery pollinose; palpi brownish; front metallic blue, brownish pollinose above base of antennae and along orbitus; orbital cilia white, about three of the upper cilia black; antennae (fig. 9) black; first joint long; third joint hardly longer than wide, evenly rounded below, pubescent; arista about two times the length of antenna with a conspicuous lamella at tip.

Dorsum of thorax blackish, with green reflections, thickly dusted with brown pollen; scutellum more greenish, its pollen gray; pleurae green, thick whitish pollen nearly hiding the ground color; abdomen with first, fourth, fifth and sixth segments black; second and third segments yellow except on dorsum; hypopygium black, the inner lamella black, finger-like; outer lamella tiny, yellow, as is also the long posteriorly projecting filament.

Fore coxae yellow, with yellow hairs and bristles; middle and hind coxae darkened on outer surfaces, still the latter nearly yellow, each with a brownish bristle on the outer surface; femora yellow, the tips of posterior pair infuscated above at tip; tibiae yellow, the posterior pair brownish on apical third; fore tarsi brownish from tip of second joint; middle tarsi (fig. 18) brownish from tip of first joint, the second joint fringed on anterior side with fine yellow cilia; hind tarsi entirely black; joints of fore tarsi as 1–9–3–4–3; of middle tarsi as 10–3–3–3–2; of hind tarsi as 5–7–4–4–3. Calypters and halteres yellow, cilia of the former long, yellow.

Wings (fig. 8) grayish hyaline.

Described from one male taken at Hooper, Utah, June 15, 1937, by D. E. Hardy, in honor of whom the species is named.

Taxonomy.—Sympycnus hardyi resembles *S. distortus* Van Duzee; it differs in the arista of *distortus* (fig. 16) being gradually enlarged on apical fifth, especially on the upper edge; in *hardyi* n. sp. the arista has a short, compact lamella at tip; the posterior femora of *hardyi* are without hairs or bristles below, whereas in *distortus* these possess a row of five or six blackish bristles of increasing length on the apical, lower half.

Sympycnus spatulatus n. sp.

Male.—Length, 3 mm.; of wing, 2.8 mm. Face showing as a silvery pollinose triangle immediately below the antennae, the eyes contiguous; front metallic, blue-green, lightly brownish pollinose above the base of antennae; antennae (fig. 15) black, first joint long, second small and rounded, third nearly twice as long as broad, its tip broadly rounded anteriorly; arista long, densely pubescent, of similar thickness throughout; orbital cilia black above, whitish below.

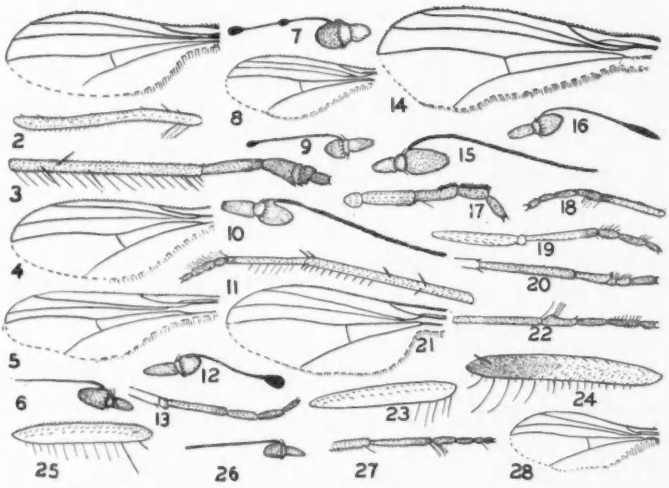
Thorax metallic blackish, dulled with brownish pollen; pleurae more greenish, its ground color showing through thick grayish pollen; abdomen metallic black, the second segment yellow on lateral margins; hypopygium large, black, globular, rounded behind, the inner lamellae black, finger-like; outer lamellae yellow, delicate.

Fore coxae yellow, the anterior surface with yellow hairs, the bristles at tip yellow; middle and hind coxae brownish, each with a black bristle on outer surface; femora and tibiae yellow, the tips of posterior femora and tibiae brownish; fore tibiae swollen, a black bristle on outer-posterior side near the base; posterior tibiae slightly enlarged at apex; fore tarsi (fig. 17) black from tip of second joint, which has a slender bristle at tip on inner side, third joint fringed above at tip with dense brownish hairs, the fourth joint similarly fringed on the whole of upper surface; middle tarsi black from tip of first joint, the second joint swollen at tip and with a few longer hairs, the third joint small, with a few hairs on the side; hind tarsi wholly blackish, the first two joints noticeably enlarged; joints of fore tarsi as, 2–8–7–5–4; of middle tarsi as, 15–6–1–2–4; of hind tarsi as, 10–12–7–4–4. Calypters, their cilia and the halteres yellow.

Wings (fig. 14) grayish hyaline; fourth vein ending in the wing tip; wing noticeably narrowed toward base.

Described from three males, the holotype taken at Hanksville, Utah, August 1, 1939, and two paratypes taken at Grouse Creek, Utah, August 30, 1939, all collections by G. F. Knowlton and F. C. Harmston.

Taxonomy.—This species is much like *N. vegetus* Wheeler but differs in the following points: In *vegetus* the antennal arista is



Sympycnus binodatus n. sp. Male, 1–3, 7. *S. hardyi* n. sp. Male, 8–9, 18. *S. spatulatus* n.sp. Male, 14–15, 17. *S. pennarista* n. sp. Male, 4, 10–11, 23. *S. fuscitibialis* n. sp. Male, 5, 12, 19, 22, 24. *S. pictipes* n. sp. Male, 6, 13, 20–21. *S. isoaristus* n. sp. Male, 25–28. *S. distortus* Van D. Male, 16.

about double the length of antennae and has a conspicuous lamella at tip; in *spatulatus* n. sp. the arista is approximately three times the length of antennae and is pubescent, of nearly equal thickness throughout. The third and fourth joints of the fore tarsi in *vegetus* lack the dense hair on upper surfaces, which is so conspicuous in *spatulatus*.

Sympycnus pennarista n. sp.

Male.—Length, 2.6 mm.; of wing, 2.8 mm. Face narrow, silvery pollinose; front metallic, blue-green, brownish pollinose above base of antennae; antennae (fig. 10), black; first joint long; third joint longer than wide; arista inserted near base, nearly three times as long as

antennae, pubescent, of nearly equal thickness throughout; orbital cilia black above, white below.

Thorax and scutellum metallic black, the dorsum dulled with brown pollen; pleurae more greenish with white pollen; abdomen black with bronze reflections, the second segment yellow; hypopygium black, its lamellae small, yellow, fringed with yellowish hairs.

Coxae yellow; middle pair darkened on outer surface; fore and middle coxae with yellow hairs and bristles upon their anterior surfaces; middle and hind coxae each with a brown bristle on outer surface; femora and tibiae yellow, the posterior tibiae slightly enlarged and blackened at tips; middle femora (fig. 23) with about 5 long yellow cilia on lower surface near base, the posterior femora have three similarly placed cilia; middle and hind femora each with one preapical bristle; middle tibiae (fig. 11) with about ten bristles on lower inner surface near apical third; fore tarsi blackish from tip of second joint; middle tarsi (fig. 11) black from tip of first joint, the basitarsus ciliated on lower surface, as long as the following four joints; hind tarsi wholly black; joints of fore tarsi as 2–5–3–3–3; of middle tarsi as 11–2–2–2–3; of hind tarsi as 7–6–5–4–3.

Calypters, their cilia and halteres yellow. Wings (fig. 4) grayish hyaline.

Described from three males; the holotype taken at Manila, Utah, September 5, 1939, by G. F. Knowlton and F. C. Harmston, and two paratypes taken at Garden City, Utah, June 11, 1939, by F. C. Harmston and V. H. Harmston.

Taxonomy.—This species is much like *Sympycnus distortus* Van Duzee, differing, however, in the following respects: The antennal arista in *distortus* (fig. 16) is approximately twice the length of antenna and is considerably widened at tip; in *pennarista* the arista is three times the length of antenna and of equal thickness throughout. In *distortus* the fourth joint of fore tarsi is twice the length of fifth joint, whereas in *pennarista* the last three joints of fore tarsi are of equal length.

Sympycnus fuscitibialis n. sp.

Male.—Length, 3.2 mm.; of wing, 2.8 mm. Face silvery pollinose, narrow below; palpi black; front dark blue, almost black, brownish pollinose above base of antennae and along orbits; antennae (fig. 12) black; first joint long; third joint hardly longer than wide, broadly rounded anteriorly; arista about one and one-half times length of antennae, a broad lamella at tip; orbital cilia white below, the brownish cilia descending about one-half eye distance.

Dorsum of thorax and scutellum blackish, with dull greenish reflections; pleurae dull green, thickly dusted with whitish pollen; abdomen blackish, with dull bronze reflections; hypopygium black, dull; outer lamellae small, yellowish, somewhat triangular, fringed with yellow hairs.

Coxae nearly concolorous with pleurae, the fore pair with scattered yellowish hairs and bristles on anterior surface; middle and hind pairs each with a black bristle on their outer sides; femora yellow, the basal half of fore pair and the apical half of hind pair blackened; hind femora (fig. 24) with long yellow cilia on lower edge and inner surface, the outer lower edge with stouter, brownish hairs on apical half; fore and middle tibiae yellow, the latter showing brownish in certain lights; hind tibiae black, the base slightly brownish in some specimens; fore tarsi (fig. 19) yellow, the last three joints brownish; middle tarsi (fig. 22) brown from the middle of first joint, the first joint with a long curled hair at tip on anterior side, the second joint swollen at base on anterior side and with about three long, crinkly hairs; fourth joint fringed along anterior edge; hind tarsi entirely black; joints of fore tarsi as 1–10–3–4–2; of middle tarsi as 12–5–5–4–2; of hind tarsi as 9–10–7–6–4. Halteres yellow; calypters yellow with narrow brown apical margin, the cilia yellow.

Wings (fig. 5) grayish hyaline; anal angle not at all prominent; wing widest about through the middle.

Described from eight males; the holotype and five paratypes taken at Currant Creek, Duchesne County, Utah, June 29, 1939; one paratype taken at Boulder Mountain, Utah, August 2, 1939, and one paratype at Wolf Creek Pass, Utah, August 11, 1938; all collections made by G. F. Knowlton and F. C. Harmston.

Taxonomy.—*Sympycnus fuscitibialis* n. sp. closely resembles *S. cilifemoratus* Van Duzee, described from Alaska; the two species differ, however, in the following points: The coxae and basal half of fore femora are greenish-black in *fuscitibialis*, whereas in *cilifemoratus* the corresponding structures are yellow. There appears to be no gradation of color in the specimens examined and for this reason *fuscitibialis* is given specific rank.

Sympycnus pictipes n. sp.

Male.—Length, 2.5 mm.; of wing, 3.2 mm. Face silvery pollinose, narrowest on lower part, yet moderately wide for a male of this genus; front metallic black; brownish pollinose above base of antennae and along orbits; antennae (fig. 6) black; first joint moderately long; third joint as long as the first, somewhat tapering, still broadly rounded anteriorly; lower orbital cilia whitish.

Dorsum of thorax and the scutellum densely brownish pollinose, the greenish ground color showing through only along the anterior margin; pleurae whitish pollinose; abdomen metallic black with greenish reflections; the lateral portions of second and third segments yellow; hypopygium metallic, greenish-black; outer lamellae small, yellowish. Halteres yellow; calypters yellow with black tips, their cilia yellowish.

Fore coxae yellow, the anterior surface more brownish with yellow hairs and bristles; middle and hind coxae concolorous with pleurae,

each with a large blackish bristle on outer surfaces; femora yellow, the apical third of posterior pair darkened; tibiae yellow; fore tarsi (fig. 13) yellow, darkened from tip of third joint, the fourth joint with short, slightly hooked hairs on upper surface; middle tarsi (fig. 20) brown from tip of first joint, third and fourth joints very short; hind tarsi with first joint yellow, the remaining joints black; joints of fore tarsi as 1–10–5–4–3; of middle tarsi as 17–6–1.5–4.

Wing (fig. 21) grayish hyaline; broad, the anal angle prominent.

Described from two males; the holotype taken at Kanosh Canyon, Utah, July 28, 1939, and a paratype taken at Leeds, Utah, October 1, 1939, both collected by G. F. Knowlton and F. C. Harmston.

Taxonomy.—*Sympycnus pictipes* n. sp. resembles *S. sobrinus* Wheeler; however, in *sobrinus* the arista is densely pubescent and distinctly enlarged near the tip; the arista in *pictipes* is without pubescence, tapering to a fine, sharp point.

Sympycnus isoaristus n. sp.

Male.—Length, 2.2 mm.; of wing, 1.8 mm. Face narrow, the eyes almost touching below, silvery pollinose; front dark metallic green, nearly black; antennae (fig. 26) black; first joint long, third joint about one and one-half times as long as broad, rounded anteriorly; lower orbital cilia whitish, the upper cilia brownish.

Dorsum of thorax and scutellum black with greenish reflections, lightly dusted with yellow pollen; pleurae dull green, the ground color showing through whitish pollen; abdomen black with dull bronze reflections, the lateral margins of second and third segments yellow; hypopygium black, the lamellae small, blackish.

Coxae yellow, the middle pair darkened on outer surface; anterior surface of fore coxae with white hairs; femora yellow, upper apical third of hind pair darkened; posterior femora (fig. 25) with a row of yellowish hairs of increasing length on lower edge, the ultimate hair much longer than those preceding it; tibiae yellow, the posterior pair darkened on apical third; fore tarsi yellow, darkened from extreme tip of third joint; middle tarsi (fig. 27) darkened from tip of second joint, first joint with two cilia at tip on anterior edge, second joint swollen at base and with three cilia on anterior surface, fourth and fifth joints with a few cilia on anterior edge; posterior tarsi entirely blackish; joints of fore tarsi as 1–6–5–3–3; of middle tarsi as 10–4–3–3–2; of hind tarsi as 6–7–5–5–4. Calypters and halteres yellow, the former with yellowish cilia.

Wings (fig. 28) grayish hyaline, the anal angle moderately prominent.

Described from three males; holotype and one paratype taken at Cedar Breaks, Utah, August 3, 1938, and one paratype taken at Manila, Utah, June 26, 1939, all collections by G. F. Knowlton and F. C. Harmston.

Taxonomy.—Sympycnus isoaristus n. sp. resembles *S. oreas* Wheeler, differing in the following respects: The fore tibiae in *isoaristus* are not swollen, whereas in *oreas* they are distinctly so; the anal angle of wing is evenly rounded and moderately prominent in *isoaristus*, whereas in *oreas* the anal margin is straight, the wing being narrow basally; in the anterior tarsi, the third and fourth joints are fringed above with long hairs in *oreas* but of plain form in *isoaristus*.

Types: Holotypes of the new species will be deposited in the U. S. National Museum; paratypes in the Utah Agricultural Experiment Station collection.

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HANDBUCH DER PFLANZENKRANKHEITEN. Volume 6. Pflanzenschutz. Verhütung und Bekampfung der Pflanzenkrankheiten. Herausgegeben von O. Appel. Fourth part, pp. 209–400, 114 text figures, 7 x 10, paper, uncut, 1939. Published by Paul Parey, Berlin. Price, RM. 8.70.

It is unnecessary to comment again on the nature and organization of volume 6 of this handbook (see the ANNALS, 32: 245 and 569, 1939, for reviews of parts 2 and 3 of volume 6). The present part 4 is of interest particularly to economic entomologists, plant inspectors, and breeders of plants for resistance against disease.

About half of part 4 deals with devices and machinery for the application of pesticides for plant protection, chiefly dusting equipment. A separate section of 26 pages is devoted to airplane dusting and spraying. References to the American literature are numerous. Fumigation equipment is discussed briefly, with special reference to citrus fumigation. Because the application of insecticidal smoke has not yet attracted much attention in the United States, we wish to call attention to the four-page section on Vernebelungsgeräte,—equipment for vaporizing a substance, such as sulfur, with heat, and blowing it into the air where it cools and solidifies in the form of an aerosol or smoke.

A section of 57 pages by Otto Schlumberger deals with seed and plant inspection.

The final section in part 4, by E. Köhler, is concerned with the breeding of plants for resistance to pathogenic bacteria, fungi and virus diseases. Part 4 closes with the first two pages of an account of plant resistance to insect pests.

—F. L. C.

THREE APHIDS OF THE GENUS BREVICORYNE VAN DER GOOT[1]

CLYDE F. SMITH,
North Carolina Agricultural College,
Raleigh, North Carolina,

and

GEORGE F. KNOWLTON,
Utah State Agricultural College,
Logan, Utah

Genus **Brevicoryne** Van der Goot

Van der Goot, Beitrage Z. Kennt. d. Holl. Blattlause, p. 245, 1915.

The genus *Brevicoryne* may be characterized as follows: Vertex moderately convex; frontal tubercles not distinctly exceeding vertex; hairs pointed; secondary sensoria circular with narrow rims; cornicles swollen, clavate, short, not distinctly longer than cauda; cauda conical; wing venation normal, media twice branched. Living on leaves and twigs of plants.

Genotype, **Aphis brassicae** Linnaeus

KEY TO APTEROUS VIVIPARA

A. Dorsum reticulated; hind tibiae with proximal portion light and distal end dusky, not uniformly colored ..... **symphoricarpi**
AA. Dorsum not reticulated; hind tibiae uniformly pale or uniformly dusky.
B. Cornicles and legs dusky; unguis 2 or more times as long as base of VI; cornicles shorter than unguis ..... **brassicae**
BB. Cornicles and legs pale; unguis subequal to base of VI; cornicles longer than unguis ..... **salixutis**

Brevicoryne brassicae (Linnaeus)

Linnaeus, Syst. Nat. Ed. 10, Tom. I, p. 452, 1758. *Aphis.*

This is a very common species on cabbage and cauliflower, often becoming abundant enough to cause serious damage. The hymenopterous parasite, *Diaeretus rapae* Curt., is often an important factor in holding *B. brassicae* in check.

The writers have collected the above aphid and its parasite in Idaho, Utah, Ohio, and North Carolina, and the Aphid from Montana, Nevada, Oregon, Washington, and Wyoming.

Gillette and Palmer (Ann. Ent. Soc. America 25: 463) give a description and good figures of the taxonomic characters of this species.

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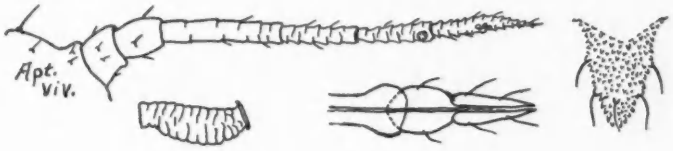
[1]Contribution from the departments of Zoology and Entomology, North Carolina State College and Utah State Agricultural College, published with the approval of the director of the North Carolina Experiment Station as paper No. 114 of the Journal series.

Brevicoryne salixutis n. sp.[2]

Apterous vivipara. Color, pale green to pale yellowish-green; antennae pale, shading to dusky on antennal VI; legs pale, tarsi dusky; cornicles pale with tip dusky; cauda dusky. Body 1.64[3] (1.17–1.75); width through eyes .45 (.39–.5); hairs on vertex .02; hairs on antennal III, .01; hairs on body .02; antennae .62 (.53–.73); antennal III, .16 (.12–.22), without sensoria; IV, .12 (.09–.12); V, .09 (.09–.1); VI, .07 (.07–.09)+.06 (.06–.08); rostrum exceeding 2nd coxae; rostral IV+V, .11 (.09–.11); hind tibiae .65 (.53–.72) and bearing hairs .02 long on the outer side; hind tarsi .11 (.10–.12); cornicles .12 (.11–.16); cauda .09 (.06–.11) for the hard portion and .11 (.09–.14) total length, bearing 2 pairs of lateral hairs and 1 dorsal one.



BREVICORYNE SALIXUTIS

Described from the holotype and 18 paratypes collected on *Salix* sp. at the mouth of Logan Canyon near Logan, Utah (holotype and some paratypes) June 13 and July 4, 1937 (C. K. and C. F. Smith; F. C. Harmston); 2 mi. west of Logan, July 22, 1936 (C. F. Smith).

This species may be distinguished from other described species of *Brevicoryne* by the characters given in the key and by the general shape of the cornicles.

Brevicoryne symphoricarpi (Thomas)

Thomas, Ill. St. Lab. Nat. Hist., Bul. 2, p. 12, 1877. *Aphis.*

This species was collected on *Symphoricarpus rotundifoliae* in Smithfield Canyon, Utah, July 11, 1937 (C. K. and C. F. Smith, F. C. Harmston); on *S. occidentalis* at Victor, Idaho, July 19, 1936 (Knowlton); Yellowstone National Park, Wyoming, July 18, 1936, and Teton Mountains, Wyoming, July 19, 1936 (Knowlton). Gillette and Palmer (Ann. Ent. Soc. America 25: 464) give a description and good figures of the taxonomic characters of this species.

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[2]The writers wish to express their appreciation to Professor M. A. Palmer for her opinion concerning this species.

[3]Measurements are given in millimeters, those in parentheses indicate paratype variations.

THE MIOCORA-LIKE DRAGONFLIES FROM ECUADOR WITH NOTES ON CORA, MIOCORA, KALOCORA, JOSOCORA AND STENOCORA

(Odonata: Polythorinae)

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Columbus, Ohio

Once or twice a year the writer receives from Ecuador or Peru a specimen or two of very small polythorine dragonflies which in size, venation and dark color pattern appear to be close relatives of *Miocora peraltica* Calvert (1917) known from the unique male genotype from Costa Rica. These specimens comprise three species, one from the watershed of the Rio Napo, one from that of the Rio Pastaza and one from La Merced, Peru.

In the E. B. Williamson Dragonfly Collection of the University of Michigan is a series of Miocora from Cristalina, Colombia, and a short series from Colonia del Perene, Peru, of the same species the writer has from La Merced, Peru, both places lying in the basin of the Upper Ucayali river. We here thank Professor F. M. Gaige, Director of the Zoological Museum of the University of Michigan, for the privilege of the study of the Williamson material.

We wish to thank our W.P.A. (Project 14703) artist, Mr. Begagy Benton, for the drawings of the wings and of four of the thorax patterns. Other drawings are by the author.

On reviewing the descriptions of species of Cora of which more than twenty have been described by de Selys, McLachlan, Karsch, Calvert, Foerster and Ris, we soon discovered that several small dark-bodied "Coras" had been described. These were so similar to each other and the descriptions were so inadequate that they were difficult to separate from each other and from the material in hand. (We did not review the writings of R. P. Longinos Navas for descriptions that might be Cora or Miocora.) This paper is an attempt to illustrate and describe the present material so well that it will not add to the past confusion. To help clear the matter we will first describe three new genera.

Kalocora, new genus

(Text fig. 1)

Genotype species= *Cora aurea* Ris, p. 24 and fig. 10 (Taf. 1), Archiv. Naturgesch., Jahrg. 82, Abt. A., Heft 9, (1916) 1918.

General characters of the subfamily Polythorinae (Odonata). Wings broad as in Chalcopteryx, width of fore wing into its length 3.25 times, of hind wing into its length 3.2 times. One strengthened antenodal which is at the arculus. Nodus about the length of one costal cell before the middle of the distance between base of wing and inner end of stigma (see fig. 1). Medio-anal link (outer end of quadrangle plus "vertical" base of Cu_2) slightly oblique to the course of the RM stem. Length of quadrangle of hind wing 1.25 times that of fore wing; each with four cross veins. Cu_2 simple as in Miocora and Stenocora. (In *aurea* Ris are a few double cells in the Cu_2 area.) A single row of cells between M_4 and Cu_1 (Ris, p. 24). Inner end of stigma slightly more oblique than outer end; height of stigma 3.5 times into length of lower side; 2 to 2.5 costal cells on the oblique inner end of stigma, about 4 costal cells following stigma.

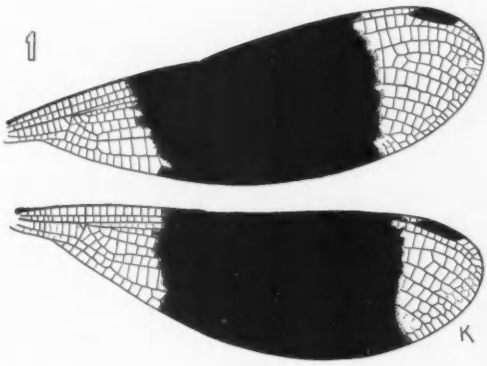


Fig. 1. *Kalocora aurea* (Ris), n. gen.

A reproduction (inked photograph), reversed, of fig. 10, Taf. 1, of Ris (1916) 1918. Wings of holotype male of *Cora aurea* Ris from Ximenes, Upper River Dagua, Colombia, 500 meters elevation, collected by A. H. Fassl.

The writer has not studied the unique male type of *aurea* Ris which is now in the Senckenberg Museum, Frankfurt am Main, Germany. The specimen is fairly well described. The fig. 10 of the wings is a photograph. Our fig 1 is traced in reverse from an enlarged photograph of Ris' fig. 10.

Kalocora differs from Miocora and Stenocora in the much broader wing, width into length about 3.25 times, while in

Miocora, Josocora and Stenocora it goes 4–5 times. It differs in the heavy metallic pigmentation of the wings which approaches the coloration of the wings of Chalcopteryx and is far different from the hyaline or lightly pigmented wings of Miocora, Stenocora or Josocora.

Kalocora differs from Chalcopteryx which it resembles in the glittering color of the wings, in that the M_4–Cu_1 area is a single row of cells (in Chalcopteryx this area with two well developed supplementary sectors) and in the lack of a fork on Cu_2.

Kalocora differs from Josocora in having a simple Cu_2. In Josocora the vein Cu_2 is bifurcate.

Kalocora differs from the smaller species of Euthore in its smaller size, single strengthened antenodal at arculus and in the unforked Cu_2.

Kalo in Greek means beautiful, which in the combination, Kalocora, means a beautiful Cora.

The type male of *Kalocora aurea* (Ris) is recorded by him as coming from the region of Ximenes, on the upper Rio Dagua, Colombia. Elevation, 500 meters. Collected May, 1909, on a rushing mountain brook by Herr A. H. Fassl of Teplitz.

Josocora, new genus

Genotype species = *Cora jocosa* MacLachlan, 1881, p. 30. Trans. Ent. Soc. Lond. for 1881.

General characters of the subfamily Polythorinae (Odonata). "Belonging to Group 1 of de Selys (Troisiemes Additions, Calopt., p. 38), in which the nodus is placed midway between the base and apex of the wings, Pterostigma black, not dilated, surmounting 6 cellules, 2½ mm. long. Twenty-six ante-cubital nervures, and 19 post-cubital, in the anterior wings. No sector between the 1st (Cu_1) and 2nd (Cu_2) sectors of the triangle; *the 2nd sector regularly and longly bifurcate.* * * * The neuration is more simple than in any other known species of the genus" (of Cora in 1881).

Josoc is a play on the species name *jocosa*.

Josocora differs from all other described genera of Polythorinae in having Cu_2 a simple fork (without a third sector in the middle between the two prongs of the fork of Cu_2). In Miocora, Kalocora and Stenocora Cu_2 is simple or with a few double cells in the Cu_2 area at most. In Cora, *sensu strictu*, and in Chalcopteryx, Euthore and Polythore it is trifurcate.

The writer has found in the literature two species described under Cora in each of which the vein Cu_2 is bifurcate. These

are the genotype of Josocora, *Cora jocosa* MacL., and *Cora klenei* Karsch, 1891.

As *jocosa* is from Ecuador and MacLachlan, because of his social inheritance distributed very few reprints, we are introducing his further descriptive notes on that species.

Josocora jocosa (MacLachlan)

(A quotation from Trans. Ent. Soc. London for 1881.)

"*Male.*—Length of abdomen, 32 mm. Length of hind-wing, 26 mm.

"Adult. Wings very slightly tinged with olivaceous, more especially on the anterior margin.

Labrum and rhinarium (clypeus) yellowish, as are also the frontal eye-margins, face otherwise black. Top of the head black, with four round orange-colored (or the posterior pair probably bluish in life) spots placed in a quadrangle. Prothorax pale blue. Thorax with a (p. 31 of the Trans. begins here) dorsal median black line dilated at each end, and enclosing posteriorly two pale spots; an ante-humeral black line indicated by a large elongate oval spot; the humeral line rather broad posteriorly, but becoming very slender; the sides with three black lines, of which the first two become confluent towards the legs; inter-alar portion black, spotted with pale blue. Abdomen black; the upper side of the first six segments pale blue, with black sutures, and on the 2nd to 6th there is a triangular black expansion near the posterior end of each. Legs black; the femora brownish internally at their base.

"♀. Unknown."

In the introductory paragraph of the article (1881) in which *jocosa* is described, MacLachlan states that on the return of Mr. Clarence Buckley to England from Ecuador last year (1880), "I obtained from him a considerable collection of Odonata, many of them most interesting and certainly new. These came from the district of the Rio Bobonaza, a tributary of the Rio Pastaza, and situated in the forest region east of the Andes."

This species has not appeared in any of the collections made by our collector, William Clarke-Macintyre, in the region of Abitagua on the upper Rio Pastaza at 1,000 meters elevation. It comes probably from a lower more tropical area.

We have introduced this genus in our study of the Miocora-like polythorine dragonflies because of its moderately small size (length of abdomen 32 mm.) and because of the simply forked Cu_2. The extensive blue color on thorax and abdomen suggests relationship to the true Coras with a trifurcate Cu_2 rather than with the species of the Miocora-like complex.

Josocora klenei (Karsch)

Cora klenei Karsch, 1891, Societas entomologica, Jour. Soc. entomologique internationale, Zurich, Vol. VI, No. 15, p. 113.

In the article carrying the description of *klenei*, Prof. Karsch gives descriptions only. No mention is made either of the collector, the locality, other than Ecuador in the title of the article, or where the specimen is deposited. Presumably it is in a Berlin collection.

At this point I wish to thank Professor Doctor O. Schneider-Orelli, Der Leiter des Entomologisches Institutes der Eidg. Technischen Hochschule of Zurich for the loan of Vol. VI of the above journal from which the writer obtained a photostat of this rare article.

"*Male.*—Abdomen 31 mm., hind wing 24 mm. long.

The nodus of the fore wing lies at the middle between the base of the wing and the inner end of the stigma; this is black, moderately "thick," 2.3 mm. long, subtending 4–5 cells; in the fore wing 24 antenodals and 23 postnodals; between the two sectors of the quadrangle lie no extra sectors, *the lower sector of the quadrangle is simply forked.*

Wings hyaline, yellowish. Head black, between the antennae of either side a dark red brown spot, clypeus and labrum muddy green, on a blackish ground, prothorax black, the middle lobe with a large greenish yellow spot on either side, the hind lobe edged on each side with a stripe of gold green. Thorax black, the pleural surface with three green stripes on each side, which spread themselves out above and across the humeral suture to the front edge of the dorsal surface (mesepisternum). Ventral surface dirty green, legs black, inner side of base green; abdomen black, the first segment with a green lateral spot, second with two green lengthwise stripes. Superior appendages with large tooth directed caudad at midlength on ventral surface.

" * * * The lack of a supplementary sector between the two sectors (Cu_1 and Cu_2) of the quadrangle and the long simple fork of the lower sector (Cu_2) of the quadrangle relates the new species near to *Cora jocosa* M'L (1881, from Ecuador), but which on account of the different position of the nodus in the fore wing may belong in another group."

In the last sentence Karsch refers to the fact that in *jocosa* the nodus of the forewing is in the middle between base and apex of the wing while in *klenei* the nodus lies halfway between base of wing and inner end of stigma. This character separates the two species structurally. By the descriptions *jocosa* is by main color effect a bluish insect while the general color of *klenei* is black with some green stripes. Apparently they are distinct species and as Karsch suggests on this character of the position of the nodus they may belong in different groups (genera). They can be left together in Josocora until more

species with simply forked Cu_2 are found. Such species if they exist may fall into two groups on the position of the nodus.

Stenocora, new genus

(Figs. 2–8)

Genotype species = *Stenocora percornuta*, n. sp.

General characters of the subfamily Polythorinae (Odonata). Wings narrow, width 4.75–5.0 times in length; one strengthened antenodal which is at the arculus; nodus almost exactly halfway from base of wing to inner end of stigma in fore wing, about one costal cell before middle in hind wing; medio-anal link slightly oblique to course of RM stem; length of quadrangle of fore wing seven-eighths that of hind wing, each with two cross veins; Cu_2 simple as in *Miocora* Calv. and 2–3 cells shorter than Cu_1 which is 15–16 cells long in fore wing and 12–13 cells long in hind wing; M_2 arises 1 to 2 R_1 cells beyond subnodus; M_3 long, usually reaching a level under the inner half of the stigma, nearly straight with only a slight forward arching at level of subnodus followed by an equally shallow concavity at outer three-fourths of length. Supplementary sectors fewest in number of any polythorine genus: two short ones behind M_{1a}, two slightly longer behind Rs and two less well defined arching beyond apex of M_4, beyond the apex of the first of which is a double row, 5–7 cells long, of M_3 cells. Antenodals 20 or 21 in hind wing, 24 and 28 in fore wing, postnodals 19 or 20. Stigma narrow, its height into length of lower side 5 or slightly more than 5 times; covering 3.5 to 5 R_1 cells; inner end of stigma only slightly more oblique than outer end; one-half to one and a half costal cells on inner oblique end of stigma; usually 4 costal cells following stigma. Antenna with third segment slender and twice as long as the second segment.

Petiole noticeably longer than in Miocora and its other relatives discussed in this article: petiole reaching to a level within a distance of two M cells basad of the inner angle of the quadrangle.

The writer has not studied the unique *Miocora peraltica* Calvert otherwise than to draw its penis. The wings of Stenocora are so little different from those of Miocora that on venational characters alone a new genus does not appear warranted, but when the characters of the male penis, abdominal segment 10, terminal abdominal appendages and antennae are taken into consideration a separate generic rating appears best. Unfortunately after five years of collecting in the general area in Ecuador where Stenocora has been found, our whole series consists of one blotter-thin very teneral male and one almost equally teneral female.

Stenocora differs from Miocora in: (1) the slightly simpler venation. There are but six extra sectors (besides M_{1a}) and the courses of the main veins are straighter which is correlated with the narrowness of the wing; (2) the narrow stigma, height

5 to 5 + times into length of lower side; (3) in the simple quadrangle, crossed but twice; (4) in the distinctly greater petiolation. The striking difference other than venation is the long slender antenna with the third segment twice as long as the second. The male differs from that sex in Miocora at once in the slender-lobed penis which would not be recognized as polythorine except for its association in an insect with unquestioned polythorine characters: in the enormous erect horn on abdominal segment 10 and in the short conical superior appendages. One other male peculiarity is the reduction of the spines of the penis shaft to a group of about twelve pairs near the head of the shaft.

Stenocora differs from Kalocora in the narrow wing, narrow stigma, simple Cu_2 space, and long third segment of the antenna.

Stenocora differs from Cora in that in the latter genus Cu_2 is forked. It differs from the remaining genera of the Polythorinae in that the quadrangle of the hind wing is only slightly (one-seventh) longer than that of fore wing.

Steno- in Greek means narrow which in the combination, Stenocora, refers to the unusually narrow wings.

Male, holotype (very teneral): abd., length, including appendages 27.5 mm., hindwg. 21 mm., fore wg. 23 mm., fore stigma 2.4 mm. long, 0.4 mm. wide. Holotype and female paratype in the author's collection.

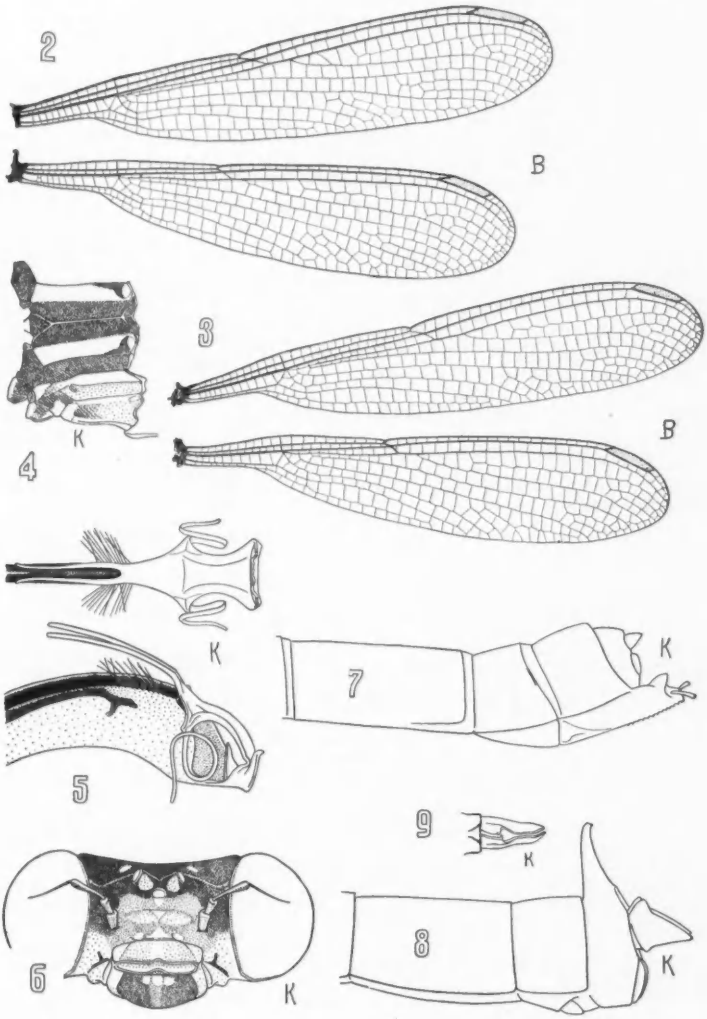
Structural characters omitted from generic description; frons with rounded edge; antennae (fig. 6) with third segment twice as long as second segment. (In the Polythorinae the first or basal segment is usually as long as the second but its posterior side is immovably sunk into the face. In higher dragonflies the first segment is usually an inconspicuous ring half buried in the face and forming a socket for what is usually termed the "first segment." The notch in apex of labium with a rectangular bottom.

The hind lobe of the prothorax a semicircular flap two-thirds as long as the middle lobe or section. Legs short, apices of third legs reach only to base of abdominal segment 1. Leg spines moderately long.

Second or posterior hamules of the second abdominal segment are broad rounded lobes half as high as the angulate lobes (anterior hamuli?) just anterior to them.

EXPLANATION OF FIGURES 2–9

2. Right wings of male holotype. Rio Jatun Yacu, Rio Napo watershed, Oriente, Ecuador, Jan., 1935. Clarke-Macintyre Coll. 3. Right wings of female allotype. Partidero, Rio Anzu, 700 meters elevation, Rio Napo watershed, Nov. 12, 1935. 4. Color pattern of allotype female, teneral. 5. Penis of holotype male, teneral. 6. Face of allotype female. 7. Abdominal segments 7–10 of allotype female. 8. Abdominal segments 8–10 of holotype male. 9. View from above of male appendages showing minute point or hook on apex of superior lobe.



Figs. 2–9. *Stenocora percornula*, n. gen., n. sp.

Penis (fig. 5) with long slender thread-like terminal and lateral lobes. In all other species of Polythorinae examined (see figures of penes of other species in this article) the penes have two short terminal lobes and almost rectangular lateral lobes which slip over the sides of the shaft and from the anterior angles of the ends of which project out and backwards a filiform secondary lobe in a single (fig. 24) or a double curve (fig. 19). The penis of Stenocora departs so widely from the penis in other Polythorinae that it would not be recognized as of that subfamily except for other accompanying polythorine characters. The usual polythorine penis characters are not recognizable. The penis is peculiar also in that the hairs on the shaft are limited to about a dozen pairs at the end of the shaft.

Segment 10 with a tall narrow dorsal horn. In our flat-as-blotting-paper specimen it is erect above the usual dorsal profile, a height two-thirds as high as the flattened segment 9. (See fig. 8.) It must be remembered that this flattening from side to side increases the height of the cylindrical body of the segment but does not increase the length of the superimposed horn. In a perfect specimen the horn may not be so erect but may point caudad at some moderate angle. The superior appendages are shown in side view in figure 8. They are so flattened that the side view of figure 8 shows all features: (1) their short length, only slightly longer than segment 10; (2) their unusual depth almost equal to the length; (3) the dorso-basal lobe sticking straight up. However, in view from above, the hind edge of the dorso-basal lobe turns entad (fig. 9) and may represent an inner spine or lobe as occurs on the male appendages of all other known polythorine dragonflies. There are no inferior appendages, which is a normal condition in this subfamily.

(I wish to call attention to the extreme teneral condition of this male. It is easily possible that the horn and superior appendages may not be fully expanded and may have a more nearly polythorine aspect in a fully expanded condition. This may apply also to the characters of the penis, but we cannot believe that, in general expansion of the latter organ, the lobes become first extremely long and slender and then shorten up to a more usual polythorine condition. In expansion the anterior portions of the insect's body expand and mature first, the posterior apex of the body last. Thus the penis may have its final form while the terminal appendages may be in the first movements of expansion.)

Color.—A uniform pale, teneral brown. We can make no estimate of any color pattern. Wings without color.

Described from the male teneral holotype taken by William Clarke-Macintyre, Esq., January, 1935, on the Rio Jatun Yacu, a small tributary of the upper Rio Napo, Prov. del Oriente, Ecuador.

Female, allotype (teneral): abd., length, including ovipositor, 24 mm., hindwg. 21.5 mm., fore wg. 23 mm., fore stigma 2.3 mm. long, 0.4 mm. wide.

Structural characters.—Antenna with long third segment as in male; posterior lobe of prothorax semicircular as in that of the male; legs slightly longer than in male, the apex of the femur reaching to apex of abdominal segment 1. Apex of ovipositor extending beyond tip of abdomen as far as length of segment 10. The widely divergent styli, seen from above, of about the length of segment 10. In the shrunken teneral the dorsum of segment 10 is caved in along the middorsal line and the two conical (?) cerci are mere flat, triangular flaps. The extreme apex of the ovipositor sheath turned abruptly downward, in side view making a terminal down-pointing tooth slightly heavier and slightly longer than the twelve or so regular teeth along the lower edge of the outer half of the valve or sheath. (See fig. 7.) The single row of heavy teeth is very different from the double row found in the female of *Cora confusa*. See description of *C. confusa* female.

Color.—On first appearance the flattened, wrinkled teneral is of a nearly uniform medium brown with face and abdominal segments 3–6 paler. On relaxation and particularly after moistening with ammonia water ("household" ammonia), traces of a color pattern appear in about three shades of brown. (See figs. 4 and 6.) Apparently the labrum is dark with a lighter area across its base. The clypeus, bases of jaws and lower genae are pale (perhaps white, pale blue or greenish in life). The frons up to the lower edge of the median ocellus and ectad to either antenna is pale brown. The vertex, occiput and genae (?) down to bases of antennae are dark (probably black in life). A pair of minute pale spots occurs halfway between lateral ocelli and occipital edge, these slightly wider apart than are the paired ocelli. A pair of larger oval spots on anterior faces of ocellar prominences. Three triangular median pale spots between median ocellus and base of clypeus, at each outer angle of the superclypeal pale spot an oval pale spot on either side of frons just above clypeal base. Under surface of head dark, probably black in life. Mouth parts pale unless apices of parts are darkening. (Prothorax mostly concealed by head and fore legs.) Meso- metathorax probably correctly shown in figure 4; an oval pale spot anterior to upper end of humeral suture below which spot is a triangular area of darker color, otherwise inner half, next middorsal carina, of mesepisternum dark, its outer half (antehumeral stripe) pale; mesepimeron dark, followed by upper half of metepisternum paler than its posterior half. Metepimeron pale, clouded with darker at its anterior end. Mesinfraepisternum dark, metinfraepisternum dark with its lower posterior quartering pale. A very pale oval spot at upper anterior angle of metepimeron. Coxae dark, edged with pale. Legs dark, shading lighter to the pale feet. Under surface of femora paler, especially towards base of leg. Abdomen an obscurely marked dark brown. Wings without color.

(The student must remember that figures 4 and 6 and the preceding notes on color pattern are from a single dried and

wrinkled teneral female and that in a well cured mature female of the same species the color pattern might be somewhat different. I believe we can count on a dark labrum, pale face, four spots on top of head and the back of the thorax dark down to the first lateral suture except for the broad antehumeral stripes pale.)

Described from the female allotype, teneral, taken by William Clarke-Macintyre, Esq., at camp No. 2 near Partidero, November 12, 1935, in the Rio Napo watershed. These spots are in the edge of the tropical jungle at an elevation of about 700–1,000 meters.

For the relationships of Stenocora see "General Thoughts" at end of this article.

Miocora Calvert

Genotype species = *Miocora peraltica* Calvert, p. 259, figs. 1–4, Ent. News, Vol. 28, 1917.

From Peralta, Costa Rica, collected by P. P. Calvert, August 8, 1909. Altitude 322 meters, on a slow moving stream. In collection of Academy of Natural Sciences of Philadelphia.

With the segregation of *Cora aurea* Ris with its unbranched Cu_2 into the new genus Kalocora and the segregation of *Stenocora percornuta* Kennedy into its new genus, Stenocora, we have to redefine Miocora because Calvert, on the strength of the unforked Cu_2, described Miocora to include all polythorine species with such a simple Cu_2. Miocora in this restricted sense can be set off as follows:

Miocora.—Characters polythorine with Cu_2 a simple unbranched vein; at times a few double cells posterior to Cu_2. Wing moderate in ratio of width to length; width into length varies from 4.2 times to 4.6 times. One strengthened antenodal at the arculus. Nodus roughly halfway between base of wing and inner end of stigma, more often so in the fore wing but nearer the base by 1–2.5 costal cells in the hind wing. Medio-anal link varying from perpendicular to course of RM stem, to being slightly oblique to same. Length of quadrangle of fore wing into length of quadrangle of hind wing on an average of 1.3 times (6:7.5 to 15 : 21); 2–4 cross veins, more often 3 in fore quadrangle and 4 in hind quadrangle. Cu_2 usually one cell shorter than Cu_1. M_2 arises a distance of half a M_1 cell to 4 M_1 cells beyond subnodus, usually about two M_1 cells distant. M_3 long in *peraltica*, its apex reaching level of inner end of stigma, in *subapicalis* similarly long in fore wing, much shorter in hind wing, in *pellucida* much shorter, the apex arched down to posterior edge of wing at a level 4–7 costal cells before inner end of stigma.

Supplementary sectors 3–4 between M_{1a} and M_2, 2–4 between Rs and M_3, 4–6 between M_3 and M_4. Antenodals, fwg. 23–26 (28 in Calvert's fig. 1), hwg. 19–26; postnodals, fwg. 20–26, hwg. 19–25. Stigma height into length of lower side 3–4 times. Obliquity of the ends of stigma similar; one costal cell on oblique inner end of stigma; 3–5 costal cells following stigma. Antenna with segment 3 only slightly longer than segment 2.

Miocora as thus defined on the species in hand, and Calvert's figure 1 (1917) and description of *peraltica*, is distinguished from Kalocora by its narrower wing, from Stenocora by a wider wing and more extra sectors in Miocora, especially the 4–6 which occur between M_3 and M_4, from Josocora by the simple fork of Cu_2 in the latter genus, from Cora by the trifurcate Cu_2 in Cora and by the same token from the wider winged genera, Chalcopteryx, Euthore and Polythore.

In our study we recognize three species of Miocora which can be separated as follows:

KEY TO SPECIES OF MIOCORA

1(2). M_3 of fore wing long, its apex reaching a level one costal cell before inner end of stigma. The black on hind wing apex reaching the costal edge, **peraltica**

2(1). M_3 of fore wing shorter, its apex falling short of the level of the inner end of the stigma by a distance of 3 to 7 costal cells..... 3

3(4). Wings without spots.....**pellucida**

4(3). Hind wing with spot under stigma that does not reach apex of wing by a distance of two apical cells.....**subapicalis**

Miocora peraltica Calvert

Male.—"Length of abdomen 34 mm., superior appendage 1.6 mm. and hind wing 24.5 mm."

Front wings: 26 to 28 antenodals, 24 to 25 postnodals, 10 cross-veins in median space, 3 cross-veins in quadrilateral, pterostigma surmounting 5 cells and parts of one or two others, its proximal edge twice as long as its distal edge.

Hind wings: 25 to 22 antenodals, 24 to 26 postnodals, 9 cross-veins in median space, 4 cross-veins in quadrilateral, pterostigma surmounting 4 cells and parts of two others, its proximal edge 1.6 as long as its distal edge."

We add from Calvert's fig. 1: 3 extra sectors between M_{1a} and M_2 (in fore wing, obscured by pigment of hind wing), 2 between Rs and M_3, 4 between M_3 and M_4.

"*Color.*—Eyes dark brown, below somewhat bluish. [Remainder of head black, a short orange streak between each antenna and the median ocellus but nearer to the antenna], labrum, genae and external surfaces of mandibles light blue, [cardines, stipites, submentum, mentum and basal two-thirds of median labial lobe pale luteous, probably also light blue in life.]

[Prothorax black, a pale blue (?) spot on either side of the middle lobe.]

Thoracic dorsum blackish; humeral suture, most of metepisternum and much of metepimeron pale bluish green, but metepisternum and metepimeron each with an [oblique] blackish tripe, less than one-half as wide as the metepisternum, but more than one-half as wide as the metepimeron. [Pectus pale, bluish green.] Unbracketed portions are from Calvert's field notes on colors of the living specimen. Bracketed notes were made later in the laboratory.

Abdomen black, a spot on each side of segment 1, a longitudinal stripe on each side of 2 and a small spot on each side of 3, pale green.

Ventral surface of thorax pruinose and traces of pruinosity on ventral surfaces of abdominal segments.

Legs: Femora superiorly, tibiae inferiorly and tarsi blackish brown, femora inferiorly and tibiae superiorly pale, perhaps bluish in life."

Peraltica was taken by Calvert in August 8, 1909, on a slow-moving stream called simply "laguna" a short distance back of Peralta Station of the Costa Rica Railway, altitude 322 meters. "Just beyond the laguna was a low woods consisting of small trees, arums, ferns, heliconias and numerous vines and creepers." Further search was made during the following days of August and in March, 1910, but no other specimens were found. Except for the series of *subapicalis* n. sp. described below all species in this Miocora complex appear as rareties in collections.

The closest relative of *peraltica* appears to be *subapicalis* from Cristalina, Colombia. Both have a spot in the apex of the hind wing and the males have similar penes (figs. 19 and Calvert, 1917, fig. 4, p. 262) in that they preserve the second loop of the filament on the anterior angle of the lateral lobe as it occurs in the majority of Polythorinae. See comments following the descriptions of *pellucida* and *Cora confusa*.

Miocora pellucida, new species

(Figs. 10–15)

Male, holotype.—Length of abdomen, including app., 29 mm., of hind wing 22 mm., of fore wing, 23 mm., of stigmas, 2 mm.

Nodus half-way between base of fore wing and proximal end of stigma; antenodals of fore wing 23, postnodals 22, of hind wing 20 and 17; quadrangles of fore wings crossed, 2 left, 3 right, of hind wings, 3 right, 4 left; extra sectors between M_{1a} and M_2, 4; between Rs and M_3, 2; between M_3 and M_4, 4, fwg., 5, hwg. The four sectors between M_{1a} and M_2 arch off the convex apex of M_2 as a bowed branch and a subbranch. In all other extra sectors the bases are free. Medio-anal link slightly oblique to course of stem RM. Stigma, height into length 4 times, proximal end slightly more oblique than distal end.

Legs short, apex of hind femur reaching base of abdominal segment 1. Penis (see fig. 12 of another male) a normal polythorine type with quadrangular lateral lobes and large internal flap but lacking the second curve of the filament attached to the angle of the lateral lobe (compare with fig. 19 of *subapicalis*); the penis of the holotype itself was not examined. Terminal abdominal appendages of the usual polythorine type with an internal acute lobe branching off just before middle of the appendage.

Color.—Face similar to that shown in fig. 13 of a female. Basal parts of labium pale, outer and terminal parts dark brown and black. Labrum dull yellow, edged below with black and with a minute black speck at center of base; exposed bases of mandibles and the hypostomal fold yellow; genae black below up to level of post clypeus, above this sharp line yellow up to level of bases of antennae, this genal yellow intruding onto outer fourth of frons; anteclypeus dark brown, postclypeus yellow except a narrow medial intrusion of black on its posterior edge; frons and top of head black except for the genal yellow cited above and a pair of conspicuous oval, very pale (white? or blue?) spots between bases of antennae and the median ocellus; rear and under side of head dead black.

Prothorax pale (bluish?) with small black areas about base of anterior lobe and with posterior lobe entirely black except a minute pale speck at each outer angle and a minute brown median basal speck.

Meso- and metathorax with dorsum blue, but with a truncate arrow-head black area balanced lengthwise on the middorsal suture (as in fig. 15 of another male). Mesostigmal area and alar carinae and their enclosed areas black; a black dot at upper end of humeral suture set off by a short semicircular blue stripe from the otherwise wholly black mesepimeron; mes- and metinfraepisterna black, irregularly edged with blue. Side of metathorax blue with an oblique irregularly edged stripe, one-third as wide as the sclerite on the episternum and a similar stripe on the epimeron. Ventral area posterior to hind legs pale pruinose with a pair of curved sausage-shaped black spots reaching along each outer edge from just back of legs to abdomen.

Legs with coxae pale, clouded with darker, trochanters pale, femora blue with outer third to half black, which color extends along dorsal side as a broad black stripe to the base of the segment; tibiae and tarsi black, wings lightly iridescent in some lights. Pterostigma black.

Abdomen and appendages black except seg. 1 with a large irregular lateral spot, seg. 2 with a lateral blue bar and a small basal spot on side of seg. 3.

Female, allotype.—Length of abdomen, including ovipositor, 37 mm., of hind wing 24 mm., of fore wing 25 mm., of stigma 2.25 mm. Antenna short as in fig. 13 of a male.

The dorsum of the middle lobe of the prothorax differs from that in the male which is normal for Zygoptera in general, in that the right and left dorsal convexities are developed into low conical elevations when viewed from the side.

Nodus half-way between base of fore wing and the proximal end of stigma, slightly nearer base in hind wing; antenodals of fore wing 24,

postnodals 23, of hind wing 21 and 21; quadrangles of fore wings crossed, right 4, left 3, of hind wings, 4 and 5; extra sectors between M_{1a} and M_2, 4; between Rs and M_3, 2; between M_3 and M_4, 5. The four extra sectors between M_{1a} and M_2 are attached basally to M_2 as described above for the male. Medio-anal link slightly oblique to the course of the stem RM. Stigma, height into length 4 times; proximal end distinctly more oblique than distal end.

Legs as in male, if anything, slightly shorter. Antenna with third segment scarcely longer than second (broken in the male holotype). Segment 9 of abdomen slightly shorter than seg. 8, measured along lower side, slightly longer than seg. 8 along mid-dorsal line. Seg. 10 0.25 times as long as seg. 9. Cerci are triangular flaps as long as the very short seg. 10. Apex of ovipositor at level of apex of cerci. Outer valve of ovipositor with 24 teeth along the outer half of its inferior edge, the apical five or six are double, the 18 anterior to these are in a fairly regular row and not "set" in alternation as in female of *Cora confusa*.

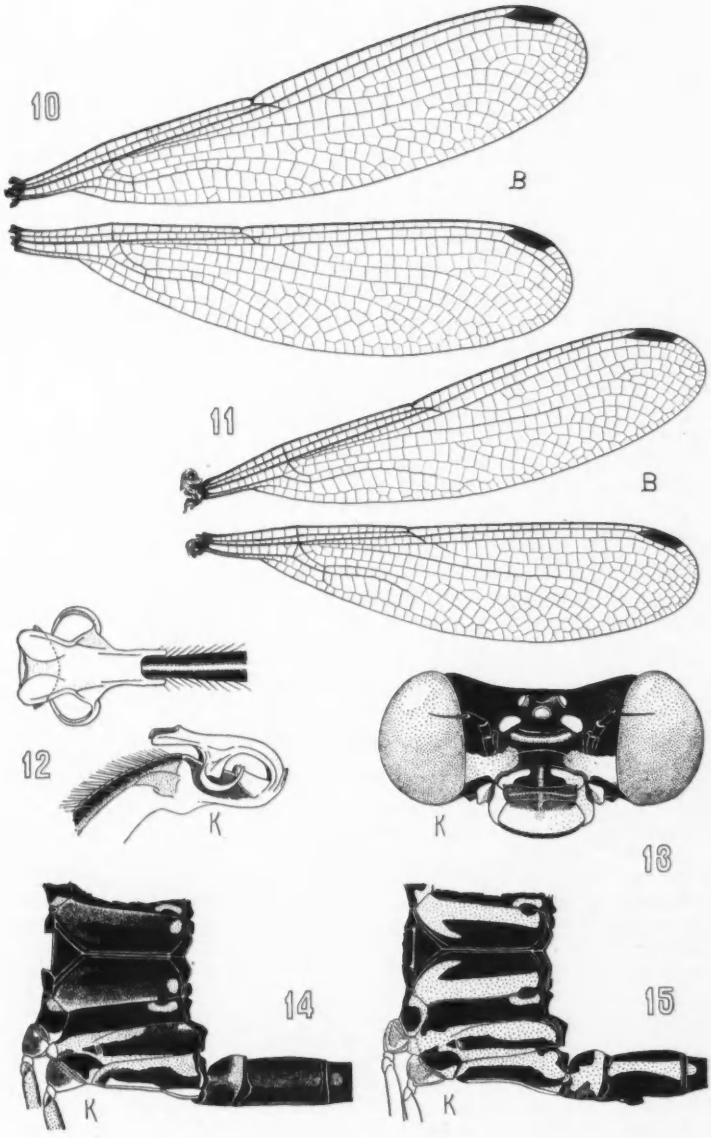
Color: Of head identical with that for the male except the middle third of the post-clypeus is black (see fig. 13 of another female). Color of prothorax as in male but pale areas more obscure. The lower side dark, edged below with pale and in upper anterior angle an oval pale spot. Meso-metathorax colored as in the male but dorsum obscured by an infusion of brown. (See fig. 14 of another female.) Venter of thorax posterior to hind legs with two curved stripes as in the male but between these a pair of smaller oval dots. Legs, wings and abdomen colored as in male.

The preceding descriptions from a male and a female papered together and now designated as holotype male and paratype female. Collected by J. H. Williamson, June 21, 1920, at Campamiento, Colonia del Perene, Peru. A pencilled note on the envelope: "In quebrada—little flowing water but fine stone bed was water soaked."

The cotype material consists of three males, two of which are of the same date and place as the types, while the third was caught at Campamiento, June 6, 1920, and has the added note (Quebrada Represa); and a second female from the neighboring town of La Merced, Peru, no further data, purchased by the writer from the Pacific Coast Biological Service, Berkeley, Calif., and now in the writer's collection. The Perene material and types are in the E. B. Williamson Collection of Dragonflies at the University of Michigan. A

EXPLANATION OF FIGURES 10–15

10. Right wings, of female from La Merced, Upper Ucayali River, Peru. No date. 11. Right wings, of male, Campamiento, Colonia del Perene, Upper Ucayali River, Peru, collected by Jesse H. Williamson, June 21, 1920. 12. Penis of above male. 13. Face of above female. 14. Thoracic color pattern of above female. 15. Thoracic color pattern of above male.



Figs. 10–15. *Miocora pellucida*, n. sp.

note in Williamson's hand on one envelope states that a male was sent to Calvert, a male to Ris, "same date" (June 21, 1920).

The data from the cotype material are almost identical with those from the types, fourteen wings were checked, two had 3 extra sectors between M_{1a} and M_2 instead of 4; all had 2 sectors between Rs and M_3; seven (50%) had 5 sectors between M_3 and M_4. The average number of antenodals is 24.5 in fore wing, 21 in hind wing; antenodals in fore wing vary from 23 to 26 and in hind wing from 20 to 22. The average number of postnodals in fore wing is 21.5, in hind wing 20.1; in fore wing they vary from 19 to 23, in hind wing from 17 to 22. The average number of cross veins in quadrangle of fore wing is 3, but the number varies from 2 to 4; in the hind wing the average is 4, but the number varies from 3 to 5.

The relationships of *Miocora pellucida* are given by our general classification. In lacking color in the hindwings it stands apart from *peraltica* and *subapicalis*. It stands apart again in the branched M_2 which is not always perfect as is shown in the male fore wing of fig. 11. This branching of M_2 occurs again in *Stenocora percornuta*, but there it involves only one branch. It stands apart again from the two in that the penis lacks the second loop of the filament on the lateral lobe (fig. 12). The latter character and the color pattern (compare with figs. 24 and 25) would seem to relate this species to the little *Cora confusa* from Abitagua. Compare figures 23 and 13 of the color patterns of the faces. It is the relationship of *Miocora pellucida* to *Cora confusa* which makes me wonder at times whether Miocora can be separated from Cora by a clear-cut definition. We present further evidence with the description of *Cora confusa*.

Miocora subapicalis

(Figs. 16–22)

Male, holotype.—Length of abdomen, including app., 32 mm., appendages 1.5 mm., of hind wing 24.5 mm., fore wing 26 mm., of stigmas 2.8 mm.

Nodus approximately half way between base of wing and proximal end of stigma, in mm. these distances are, fwg., 12 + 11 mm. base to stigma, hwg., 10 + 11.5 mm. Antenodals of fore wing 29, postnodals 25; quadrangle of fore wings crossed 4 times in each, of hind wings 3 in left and 4 in right. Extra sectors between M_{1a} and M_2, 4; M_2 and M_3, none in fwg., 2 short sectors in hwg.; M_3 and M_4, 4 in fwg., 3 in hwg. All extra sectors with free bases. Medio-anal link slightly oblique in fore wings, vertical to course of RM in hind wing. Stigma in fore wing with proximal end slightly more oblique than distal end

and fully twice as long as distal end, in hind wings obliquity of proximal end and difference in length slightly less pronounced. Costal edge of stigma much arched with the contour of apex of wing while the R_1 edge is straight. Thus all stigmas are decidedly narrower at outer end than at basal end.

Legs short, apex of femur barely reaching base of abdominal segment 1. Penis (see fig. 19 of another male) with the second loop of the filament on anterior angle of the lateral lobe as in *peraltica* and in most other polythorines; the internal flap is larger than usual; the penis of the holotype itself was not examined. Appendages of abdominal segment 10 are of the usual polythorine Y-type with a curved, pointed internal branch. Such are alike from species to species in Miocora and are similar in Cora.

Color.—Similar to that shown for a cotype male in figures 20 and 22, but differing in some details. In the holotype the post-clypeus is entirely black and the pale humeral stripes are less sharply defined.

In detail the color of the holotype; labrum black with two oval pale spots at either side of base; ante-clypeus dark brown, post-clypeus black; frons and vertex and under surface of head black. The following are pale: two spots on labrum (yellow?), the base of the mandible and of hypostoma pale bluish green, gena yellowish on upper half below base of antenna and black on the lower half next the blue hypostoma. In the holotype this genal black band extends from the eye to the lower angle of the frons completely separating the blue below from the yellow above. On the vertex between median ocellus and the antenna is a small oval brown spot on either side. A note on one envelope speaks of the eyes as black. The labium is vigorously colored, mentum and submentum white except the outer lobes and the two free points of the mentum jet black.

Prothorax black but on lower side shading into a paler color probably bluish in life.

Meso-metathorax black with the following areas reddish brown in the dried type: a narrow ante-humeral line reaching from the mesostigma to the depression at upper end of humeral suture (in fig. 22 it passes around this), forward half of metepisternum, an irregular pale band along second lateral suture (at level of stigma it straddles the suture, but passes back of it onto the metepimeron at the upper end of suture), lower edge of side which shows some blue. Infraepisterna and coxae black with some irregular edging of paler. Ventral surface heavily white pruinose. Legs and coxae pale with white pruinose edges, trochanters pale, femora bronzy brown-black, paler underneath and at bases, tibiae and tarsi black.

Wings hyaline, but base to quadrangle and costal edge to M_{1+2} before nodus and to R_1 beyond nodus yellow. Stigmas dark brown. A nearly circular brown spot under stigma of hind wing. This extends from a level of two M_1 cells before the stigma to within one cell of apex of wing from vein M_1 (with extension up under stigma) to M_2. The central area is much darker than the border. A much paler spot lies in the M_1 area under the stigma *of the fore wing* for a length of three M_1 cells. This is so pale it is not noticed except in very mature individuals

and when studied under the microscope. The position of these spots in not reaching the apical edge of the wings suggested the specific name *subapicalis*. In *peraltica* the spot reaches the extreme edge of the wing. (See Calvert, 1917, fig. 1.)

Abdomen black except for side of segment 1 pale brownish and a vaguely bordered area on side of base of segment 3.

Female, allotype.—Length of abdomen, including ovipositor, 25 mm., of hind wing, 24 mm., of fore wing, 25 mm., of pterostigma, 2.6 mm.

Antenna with third segment 1.5 times as long as the second and when laid on the face the apex of segment 3 barely surpasses the orbit of the compound eye. The lateral halves of the dorsum of the middle prothoracic lobe are slightly inflated but do not bulge up into conical prominences as in the female of *pellucida*; the hind lobe is regularly semicircular.

Nodus halfway between base of fore wing and proximal end of pterostigma; in hind wing it is slightly closer to the base, the distances, base to nodus 10 mm., nodus to inner end of stigma 11.5 mm. Antenodals, fore wings, 26, postnodals 26; antenodals, hind wings, 22, postnodals 25; quadrangles of fore wings crossed, right 3, left 4, of hind wings, right 4, and left 4. Extra sectors between M_{1a} and M_2, 4, between M_2 and Rs, fwg. 0, hwg. 1, between Rs and M_3, 2, between M_3 and M_4, fwg. 2, hwg. 4. The four between M_{1a} and M_2 are not attached basally to M_2 and do not form branches of that vein. Medio-anal link very slightly oblique to course of RM stem in fore wings, vertical in hind wings. Stigmas as in male, the proximal side twice as long as distal side and more oblique so that the pterostigmas are about twice as high at inner greatest height as at outer end; costal side strongly convex, the R_1 side straight.

Legs short with apex of hind femur not reaching base of abdomen. The lengths of abdominal segments 6 to 10 in millimeters are as follows: 3.5 mm., 3.0 mm., 1.5 mm., 1.75 mm., and 0.5 mm. Apex of ovipositor extending beyond end of abdomen as far as the length of abdominal segment 10; about 39 teeth along outer three-fifths of lower edge of valve; the row is not exactly regular as about every other tooth is ectad to the main row which gives a slight "set" as of the teeth of a cross-cut saw, the apical tooth is not larger than the others; styli curved, diverging and equal to segment 10 in length.

Color.—Face very close in color pattern to that of the male shown in figure 20, except that the pale spots of the labrum are on its outer angles and the outer edge of the basal segment of the antenna is pale. For the thorax the color of dorsum is similar to that of figure 21 (which is of another female), while the color of the side resembles that of figure 22.

In detail the color is as follows: labrum black with a pale dot at

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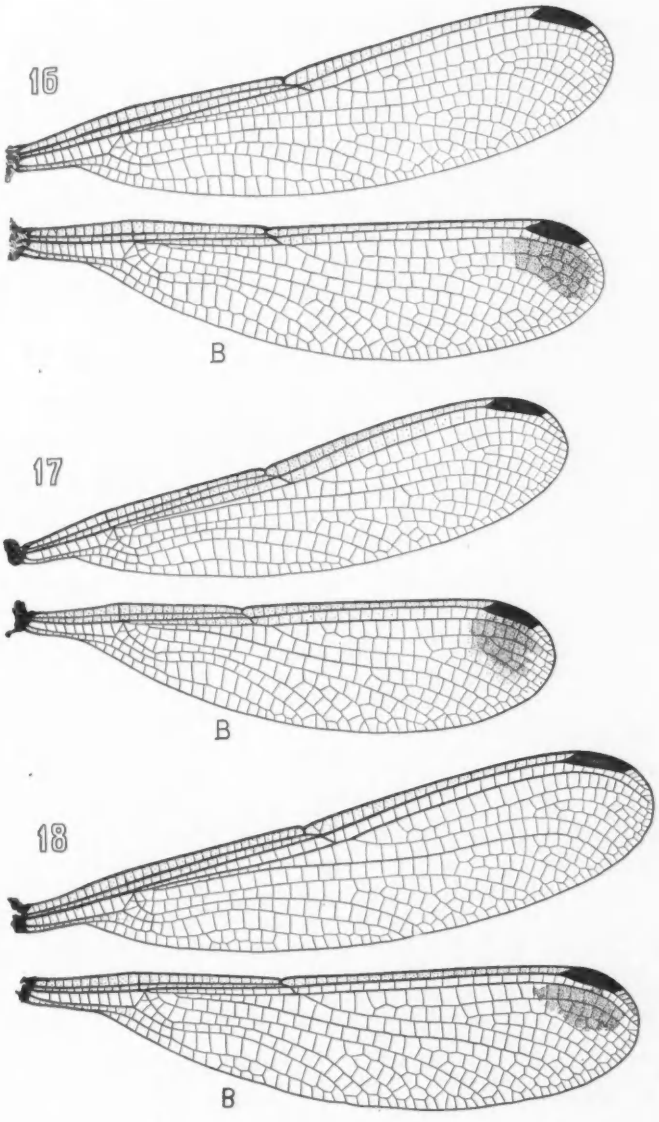
EXPLANATION OF FIGURES 16–18

16. Right wings of paratype male from Cristalina, Colombia, collected by J. H. and E. B. Williamson, Feb. 12, 1917. 17. Right wings of paratype female, same data, but coll. Feb. 15, 1917. 18. Left wings of another male, same data, but coll. Feb. 12, 1917. *See double cells in Cu_2 area.*



Figs. 16–18. *Miocora subapicalis*, n. sp.

each end; anteclypeus black with brown median area; postclypeus black with minute yellow dot at each end. Bases of mandibles bluish yellow; lower gena black from eye to clypeus, upper half of gena yellow. Frons and vertex black with outer edge of basal segment of antenna yellow and a pair of yellow dots, one each, between base of antenna of either side, and the median ocellus. Rear and lower sides of head black. Labium pale with outer labial lobes and the lobes of the mentum jet black.

Prothorax black with a large lateral blue area, crossed in its middle by a thread of black and its upper end edged with orange, its bottom end eged with pale yellow.

Meso-metathorax with dorsum pale brown laterally, this color extending across the humeral suture over the upper third of the mesepimeron. The middle third of this dorsal area, covering the mid-dorsal carina, black as are the alar carinae, the areas they surround, and the upper fifth of the humeral suture. (See similar pattern on fig. 21.) Sides of thorax pale brown with lower two-thirds of mesepimeron black and an irregularly shaped and vaguely edged black band on the middle two-fourths of the metepisternum and another on the lower two-thirds of the metepimeron, a pattern very similar to that in figure 22. Infraepisterna mottled. Coxae pale, their edges pruinose; trochanters pale, femora darker toward apex, lighter toward base and on lower side; tibiae and tarsi black.

Wings suffused with yellow throughout, from base to quadrangle heavily as also along costal edge. Hind wing with a diffuse brown spot under stigma reaching about halfway to hind edge of wing and to within the length of one cell of apex of wing. A slight darkening below stigma of fore wing. The dark spot on hind wing a metallic bluish green in certain lights. The extreme apical edge of all four wings opaque white in certain lights. Stigmas dark brown.

Abdomen black with a large pale area on side of segment 1, a dot on side of base of segments 3–5, and a narrow pale line along sides of segments 2 and 3.

The preceding descriptions from a male and a female papered together and now designated as holotype male and allotype female: collected by J. H. and E. B. Williamson, February 12, 1917, at Cristalina, Colombia, deposited in Williamson Dragonfly Collection, University of Michigan. Notes in E. B. Williamson's hand-writing on other envelopes read, "This species seen today (Feb. 17, 1917) only in gully, rare or wanting on main Quebrada

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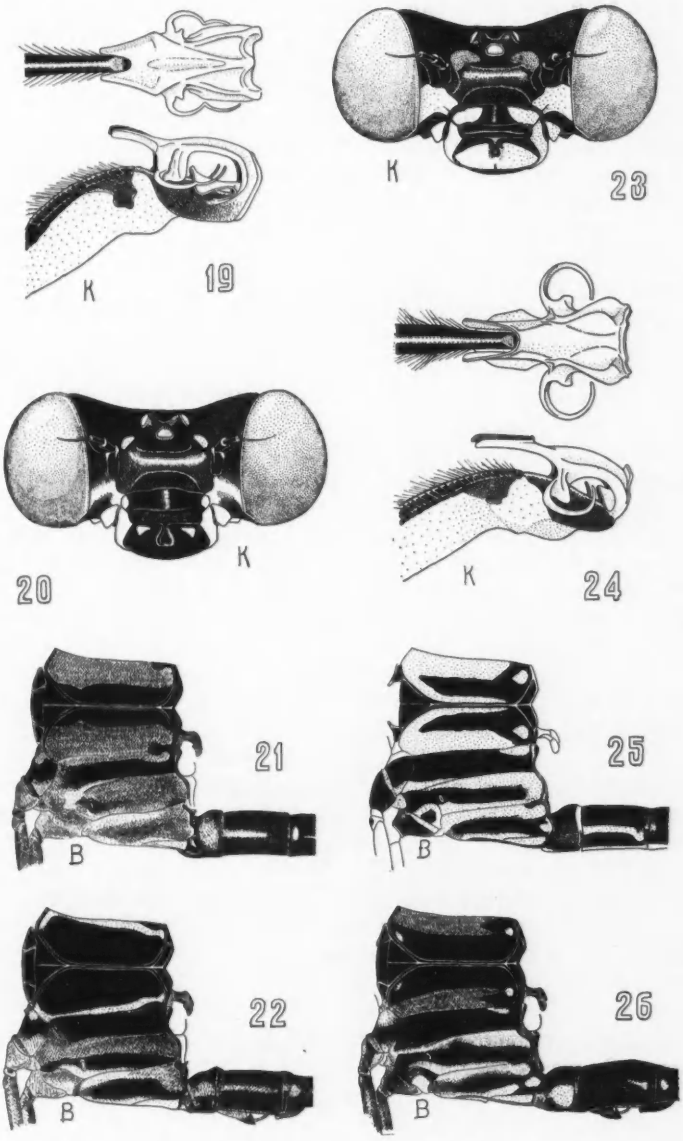
EXPLANATION OF FIGURES 19–26

19. Penis, paratype, Cristalina, Colombia, coll. by J. H. and E. B. Williamson, Feb. 19, 1917. 20. Face, male paratype, same place, Feb. 12, 1917. 21. Color pattern of paratype female, same data as for No. 20. 22. Color pattern of same male as No. 20.

23. Face, male paratype, Abitagua, Rio Pastaza, Ecuador, coll. by W. C. Macintyre, Nov. 7, 1936. 24. Penis, same male as No. 23. 25. Color pattern, allotype female, Abitagua, Rio Pastaza, Ecuador, coll. W. C. Macintyre, Nov. 10, 1936. 26. Color pattern, same male as Nos. 23 and 24.



Figs. 19–22. *Miocora subapicalis*, n. sp.
Figs. 23–26. *Cora confusa*, n. sp.

where blue thorine (Cora?) is found." A second note: "Male thorine (Miocora) has wings with purplish pink reflections, at times brilliant in sun, but prefers shade and rests at varying heights and on various supports, much like a Hetaerina, wings always closed." Third note, male: "Calopterygine with black eyes and dull Heteragrion-like colors. Humeral stripe dull blue. Thoracic side, below and behind, brown, dull. Abdomen black." Fourth note, male: "Thorax black, pale markings dull blue, humeral stripe the brightest."

The preceding notes were on envelopes of material at Mariquita where the species was first found. The following were on envelopes of material from Cristalina where the great number of specimens was obtained: "Flight abrupt. Position pugnacious. Wings folded and brought together to give effect of one wing only. Often rests on support with body leaning to one side. Prefers twigs or limbs but alights also on leaves. Not timid—may frequently be taken with fingers. Ceases flying early in day." On another Cristalina envelope: "Female oviposits in solid but damp logs over water. One of these was observed for some time. From one position of legs abdomen was moved over an area about 0.75 inch in diameter. The ovipositor was thrust full length into minute crevices or in the grain of the log, requiring some force for insertion and removal."

The cotype series consists of 5 males and 2 females taken by J. H. and E. B. Williamson, February 3, 1917, at Mariquita, Colombia. Also about 110 males and 8 females taken by the Williamsons, February 12 to 20, 1917, at Cristalina, Colombia. A note on a slip of paper in the box with the material states, "Gave Ris, 12–31–20, two males and one female of Miocora, Cristalina, 2–16–'17." Other notes on another slip: "Given Needham 3 males, 2–19–'17 and male and female, 2–12–'17;" also, "Male and female, 2–12–'17, given Laidlaw."

This is the only case in which any collector has obtained more than a half-dozen or so specimens of any species in this Miocora-complex. We feel that part at least of the credit for the large series should go to thorough collecting by expert collectors who recognized early that this "dull" inconspicuous dragonfly was a choice find.

We have examined each specimen of this series under the binocular for any peculiarities of the Cu area, also for large and small specimens, darkly colored and lightly colored individuals,

etc. Besides notes on peculiar individuals we have selected five of the ten envelopes that contained both a male and a female and have summarized what was found in their venation.

First, the following on color in the wings is on data taken from nine pairs papered as such: five males and three females had a spot in the fore wing, smaller than that in the hind wing and so pale as to easily escape casual inspection, but a spot in the same location with regard to the wing tip. Three males and six females had the extreme (one apical cell wide) apex of the wings an opaque white. This easily escaped notice unless flashed exactly right. Apparently it was pruinosity associated with age. Teneral specimens did not have it nor did such have an apical brown spot in the fore wing.

Two males in this series of 9 pairs had double Cu_2 cells, one double cell in one hind wing for each insect.

The following are some data on the five pairs picked at random (in envelopes when selected): average length of abdomen, male, 33.8 mm., female, 25.5 mm., average length of hind wing, male, 25.5 mm., of female, 24 mm.; average number of antenodals, male, fwg., 28.4, hwg., 23, of postnodals, male, fwg., 25.4, hwg., 24.4; average number of antenodals, female, fwg., 26.4, hwg., 19.6, of postnodals, female, fwg., 23.6, hwg., 22.8. Quadrangle crossed, male, fwg., 4 times in all five males, male, hwg., average of 4.25 times (two crossed 5 times, two, 4 times, one, 3 times); female, fwg., 4, crossed 3 times, one, 4 times, hwg. all crossed 4 times.

In the matter of extra sectors the average number in space M_{1a} to M_2 is 3 in both male and female for the fore wing and 4 for the hind wing: M_2 to Rs no sector in fore wings, 4 males had 1 or 2 in hind wing, 2 females, one with 1, one with 2 in hing wing: Rs to M_3 male average, fwg., 2.6, hwg., 2.4; female, average, fwg., 2.8, hwg., 2: M_3 to M_4 (usual number in both male and female, 4) male, fwg., average 2.2, hwg., 3.8; female, average, fwg., 3.8, hwg., 3.8.

The nearest known relative of this species of Miocora is probably *Miocora peraltica* Calvert (1917). The penes are similar in that both have lateral filaments with two succeeding curves or loops as are found in most other species of the Polythorinae. (See Calvert, 1917, fig. 4, on p. 262 and our fig. 19.) They are further similar in that there is a conspicuous spot in the apex of the hind wing. In the *peraltica* specimen the color in this apical spot extends to the edge of the wing. In *sub-*

apicalis it does not reach the apical edge of the wing by a distance of the length of the marginal row of cells. *Subapicalis* differs from *pellucida* of Peru in that in the latter the penis lacks the second loop of the lateral filament (fig. 12) and the wings are without markings. *Pellucida* differs also from *peraltica* and *subapicalis* in the tendency for the extra sectors between M_{1a} and M_2 in the *pellucida* wing to become attached as branches of M_2. In *peraltica* and *subapicalis* this tendency toward branches on M_2 is much less in evidence.

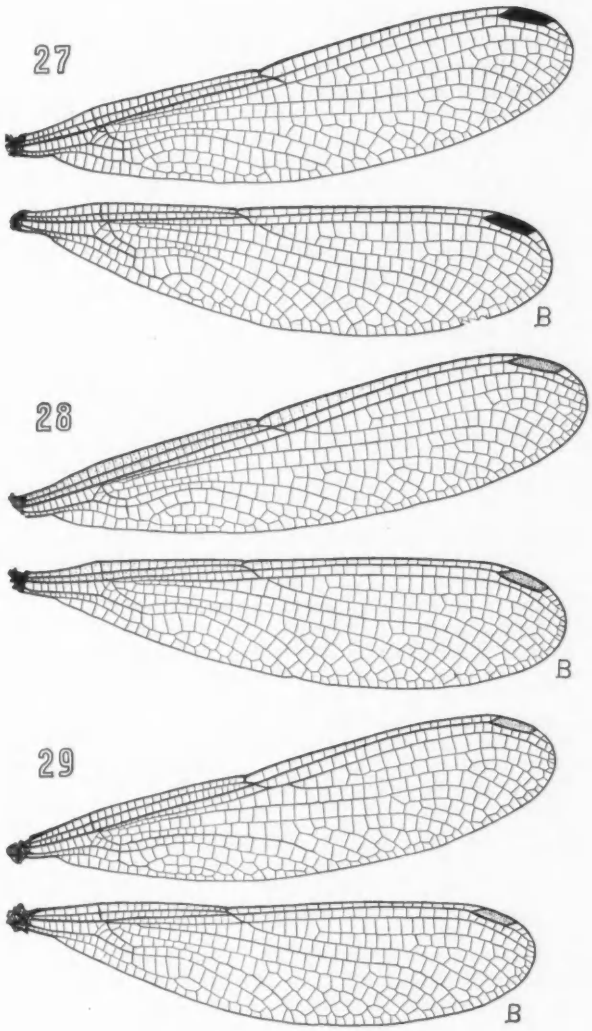
Cora confusa new species

(Figs. 23 to 29)

In this study of the various small polythorine species which have a Cu_2 that is not trifurcate but is either a single vein, a single vein followed by a few double cells, or a Cu_2 which is merely bifurcate, we were puzzled by certain specimens from the Abitagua region of the upper Rio Pastaza of the eastern slopes of the Andes in Ecuador. The fore wings in this series were definitely in the genus Cora but by our generic divisions the hind wing in such a specimen might have the character of Josocora or Miocora. We do not have specimens and distributional data enough yet to decide whether this is a "hybrid" population or a "connecting link" species between three groups as cited above, Cora being the third. We describe the specimens and name the group *confusa* because of the evident state of the germ plasm in this population.

Male, holotype.—Length of abdomen, including appendages, 31 mm., of hind wing, 23 mm., of fore wing, 24 mm., pterostigma, 2 mm. long, 0.5 mm. wide.

Structural characters.—Antenna short, apex of segment 3 barely reaching orbit of compound eye, third segment less than twice as long as second. Frons and occipital area of top of head with much long brown hair. Prothorax with right and left halves of middle lobe somewhat inflated when viewed laterally, sides smoothly convex from top to bottom. Legs short, apex of hind femur scarcely reaching base of abdomen. Penis not studied in holotype but from the other male studied (fig. 24) its two peculiarities are the rather long apical lobes (compare with Miocora, fig. 19) and with the short, heavy, and, when viewed from below, circular filaments of the lateral lobes. The penis thus is curiously similar to that of *Miocora pellucida* n. sp. from Peru (see fig. 12). The internal flap is the shortest we have found among these various species. Abdomen slender; the superior terminal appendages, branched forcipate as usual in the Polythorinae, but the internal branch with a dull apex and a quadrangular shape when viewed



Figs. 27–29. *Cora confusa*, n. sp.

27. Wings of male, same data as for figs. 23, 24 and 26. 28. Wings of allotype female, same data as for fig. 25. 29. Wings, paratype male, Rio Pastaza, April 2, 1936. Coll. W. C. Macintyre.

from above, thus the internal contour of the fork is a smooth rounding curve but the external contour is a right angle. It is the first so decidedly angulate polythorine appendage we have seen.

Wings.—Nodus of fore wing halfway between base of wing and inner end of stigma, the distances of the two halves being 10.5 mm. and 11 mm. Stigmas very slightly narrower at distal end than at proximal, but anterior or costal side not convex as in *subapicalis* proximal side slightly more oblique than distal side. Quadrangles crossed 4 times, except the right hind quadrangle 5 times; comparative length of fore and hind quadrangles as 1.5 to 2. Extra sectors, M_{1a} to M_2, fwg., 3, hwg., 3; Rs to M_3, 2; M_3 to M_4, fwg., 5, hwg., 4. Cu_2 in fore wings trifurcate thus holding two rows of cells, the lower row 3–4 cells long, the upper row 8–9 cells long. *Cu_2 in hind wings simple*, right wing with one double cell in the Cu_2 row, left wing with two such double cells.

Color.—In general black or very dark. Labrum yellow, edged below and above, and a vertical line down its middle, black; clypeus black with obscure lighter sides on horizontal surface; bases of mandibles and hypostomal fold back of base of mandible yellow; gena below base of antenna to level of postclypeus yellow, below this, black. Top and under side of head black with a large very dull brown spot (a pair) on each side between median ocellus and base of antenna.

Prothorax black with large brown oval spot covering the whole side of middle lobe.

Meso-metathorax with inner half of each mesepisternum black and outer half obscure dark brown; mesepimeron black except a narrow pale area about sulcus at upper end of humeral suture and some pale brown about its lower end; side of metathorax pale brown with a broad obscurely edged, irregular stripe down the episternum and another on the epimeron; infraepisterna and coxae mottled brown and black. Legs black with inner surface of femur pale brown. Ventral surface posterior to hind legs pale brown and pruinose with a pair of sausage-shaped stripes, one along each lateral edge. Wings hyaline, faintly tinged with yellow from base to nodus. Pterostigma black.

Abdomen black with a pale spot on lower side of segment 1, a narrow line along side of 2 and a minute pale dot at base of side of segment 3.

Female, allotype (teneral but color pattern showing; thorax badly wrinkled and shrunken).—Length of abdomen including ovipositor, 27 mm., of hind wing, 24 mm., of fore wing, 25 mm., of pterostigma, fwg., 2.5 mm., hwg., 2.2 mm., height of stigma, fwg., 0.6 mm., hwg., 0.5 mm.

Antenna as in male, short, the third segment but slightly longer than the second segment and its apex scarcely reaching orbit of eye. In lateral view in this wrinkled teneral the middle lobe of the prothorax is only slightly inflated above, if at all, but on top of each half of the middle lobe is a minute tubercle or nipple in side view; the side of the prothorax is smoothly convex from top to bottom; hind lobe regularly semicircular.

Nodus in fore wings exactly halfway between base of wing and proximal end of pterostigma, in hind wing slightly closer to the base,

the measurements are 10 mm. and 11 mm. Antenodals, fore wing, 27, postnodals, 20; hind wing, 25 and 22. (These data are of the left wings of the single female. See fig. 28 for the right wings.) Extra sectors between M_{1a} and M_2, fwg., 3, hwg., 4; between Rs and M_3, fwg., 2, hwg., 2; between M_3 and M_4, fwg., 5, hwg., 5. The three or four extra sectors between M_{1a} and M_2 are not attached as branches to M_2 as in *Miocora pellucida*. Quadrangle crossed 4 times in fore and hind wings: in fore wing 1.4 mm. long, hind wing, 1.8 mm. Medio-anal link very slightly oblique to course of RM stem. Stigmas noticeably narrow, outer end narrower than inner end, inner side very much more oblique than outer end, upper (costal) and lower (R_1) sides equally slightly convex; stigmas each subtending 4 R_1 cells. In fore wing Cu_2 trifurcate, lower row of cells within fork 3 cells long, upper row 7 cells long; ***hind wing with Cu_2 bifurcate***, the lower branch 5 cells long, the upper branch 10 or 11 cells long.

Legs short, apex barely reaching base of abdomen, lengths of segments 6 to 10, in millimeters are as follows: 4 mm., 4 mm., 1.5 mm., 1.0 mm., 0.6 mm. Apex of ovipositor extending beyond segment 10 as far as length of abdominal segment 10; teeth on edge of outer half of ovipositor sheath as follows, starting at tip of sheath; 1 large tooth, then 8 pairs of teeth, then 28 single teeth. The teeth are "set" as on a cross-cut saw. The two teeth of a pair point each out and away from the other. The 28 single teeth alternate in "set," every other one directed entad, the alternate ones ectad. Styli equal to segment 10, probably curved in mature females. Cerci, flat triangular flaps.

Color.—Because of the teneral condition with all surfaces warped, wrinkled or ironed out, the partially developed color pattern cannot be vouchsafed by either artist or author. Figure 25 is artist Begagy Benton's interpretation, which checks as closely as we are able to check, with the surface conditions such as they are.

Labrum, pale yellow (?) edged below and along base with narrow lines of black and as in the holotype a narrow mid-vertical line; clypeus black with perhaps a small pale spot at each end of the post-clypeus; frons and vertex black, a small median brown spot below median ocellus and a pair of oval brown spots one on either side between base of antenna and the median ocellus; upper half of gena pale (orange?), lower half black; base of mandible pale as also the hypostomal fold at mandibular articulation. Labium smoky brown with lateral lobes and terminal lobes of ligula jet black. Under surface of head black.

Prothorax dark with large oval pale spot covering the side of the middle lobe. Meso- and metathorax pale brown (color partly due to poor preservation) with middorsal keel narrowly black as are the antealar carinae; each pale mesepisternum with a broad black stripe one-third as wide as the sclerite extending from alar carina down the sclerite's middle almost to the mesostigmal carina, the upper end as wide as the episternum and enclosing a large pale spot. Mesepimeron black except upper anterior angle and lower posterior angle pale. Metepisternum pale with a slightly diagonal black stripe extending from its anterior end, to end free above at some distance below the alar keel. Metepimeron similarly colored but the dark stripe forked just

in front of alar keel. (See fig. 25.) Ventral surface posterior to hind legs probably pale with a dark sausage-shaped band along either outer edge. Legs with tibiae and tarsi dark, femora lighter (very poor preservation). Wings without suggestion of color. Abdomen with the usual pale spot on lower side of segment 1, an illy defined stripe the length of segment 2 and a small circular pale spot on side at base of segment 3, otherwise black.

Descriptions from holotype male, mature, from Abitagua, upper Rio Pastaza, east of Andes, Prov. del Oriente, Ecuador, elevation 1,100 meters, 20–XII–'39, and allotype female, teneral, same locality, 10–XI–'36, both collected by Professor William Clarke-Macintyre of the University of Quito. Deposited at present in the author's collection.

The cotype material consists of: (1) one mature male, Abitagua, Rio Pastaza, Oriente, Ecuador, 7–XI–'36 and, (2) one very teneral male, ironed flat, April 2, 1936, Rio Pastaza, Oriente, Ecuador. The wings of this appear in figure 29, of the female allotype in figure 28, of the cotype mature male in figure 27. All were collected by Professor William Clarke-Macintyre.

The cotypes agree with the two type specimens in having one or both hind wings with a peculiar Cu_2. In (1) the left hind wing has a simple bifurcate Cu_2. The other hind wing (fig. 27) has a proper trifurcate Cu_2. In (2) the left hind wing (fig. 29) is unforked except for a single oval cell, while the right hind wing has a simple unbranched Cu_2 except for two such oval cells. The immature dorsal color pattern of the thorax (fig. 25) suggests the arrowhead pattern of *Miocora pellucida* (figs. 14 and 15). The pale labrum and pair of large oval pale spots on the ocellar region suggest the face of *pellucida* but by Cu_2 in both fore and hind wings *pellucida* is a true Miocora while by Cu_2 in the fore wings *confusa* is a true Cora. To what genus do the hind wings of *confusa* belong? The question will have to remain unanswered until some reincarnation of Williamson goes down and brings back a long series.

SOME GENERAL THOUGHTS

We believe that in working over this series of species we are working with some of the most primitive types of living dragonflies. They are small insects which follow the writer's conclusions (Kennedy, 1920) when reviewing the Zygoptera for a thesis (never published in its entirety) that the broad-

winged, richly veined Agriidae were fairly recent forms and that the more primitive Zygoptera would be found among the smaller, more simply veined forms. Tillyard swung over to this idea after studying the writer's thesis for two days at Cornell University in the early 1920's. (Tillyard, 1923, p. 295.) The later discovery of Permian and other fossil Zygoptera confirmed this view which the writer had worked out on a study of genitalia and venation.

The curious genus Stenocora of this article, known only from the teneral holotype and allotype, is probably, because of its high specializations, a persisting but very primitive form at the very base of polythorine development. It is extremely specialized in its long antennae, peculiar horn on segment 10 of the male and especially so in the penis, which does not even look generally polythorine. Along with these high specializations which so frequently accompany primitive types of animals, is an extreme simplicity of the wing that with its straight and simple Cu_1 and Cu_2 and the few extra sectors is polythorine only in the shape of the quadrangle. It is further generalized in its long petiole. If our theory is correct, theoretically Stenocora is a very primitive dragonfly, a living mesozoic fossil, from before the Eocene which already had broad-winged Polythorinae. (See Cockerell, 1930.) Stenocora appears as ancient among the polythorines as Caliphaea of southeastern Asia appears among the Agriinae.

We have wondered for some years why South America did not present us with such primitive rarities. Here we appear to have one such living fossil which was not recognized as such until we tried to fit those two frail tenerals into the frame of the Miocora-complex.

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Karsch, F. 1891. Neue Odonaten von Ecuador. Societas entomologica (of Zurich), 6 (Oct.): 113. (Desc. *Cora klenei*, n. sp.)

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EMBRYONIC MEMBRANES, YOLK CELLS, AND MORPHOGENESIS OF THE STONEFLY PTERONARCYS PROTEUS NEWMAN[1, 2]

(Plecoptera: Pteronarcidae)

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In an earlier paper (Miller, 1939) on the embryology of the stonefly *Pteronarcys proteus* Newman, the author described the egg, oogenesis, oviposition, and incubation, provided a synoptic table of the entire embryonic development, and dealt in detail with the early stages up to the formation of the embryonic rudiment (ventral plate or germ disc). The present paper continues the account with a description of the embryonic membranes, the yolk cells, changes in the yolk, and details of embryonic morphogenesis. Included under the latter head is an account of the pleuropodia.

References to the successive growth stages of the embryo are made by means of the Roman numerals I to X assigned to them in the first paper, where they were described and figured (pages 576 to 583, and plate I). Descriptive names there given to the stages are as follows: I, spheroid and ovoid embryo; II,

[1]Most of the subject matter of this paper formed part of a thesis presented to the Faculty of the Graduate School of Cornell University, June, 1938, for the degree of Doctor of Philosophy. In this revised and augmented form, the account of the pleuropodia is a major addition.

[2]Research Paper No. 680, Journal Series, University of Arkansas.

pyriform and slipper-shaped embryo; III, protocephalic-lobe, unsegmented embryo; IV, arched, segmented embryo; V, limb-bud stage; VI, unconsolidated, immersed embryo; VII, consolidated, immersed embryo; VIII (following blastokinesis), lateral embryo; IX, head-to-tail (coiled) stage; X, spiral embryo (complete).

Materials and methods were described in the first paper.

The Embryonic Membranes

THE SEROSA AND SEROSAL CUTICLE

The prospective serosal cells become recognizable during the primary-epithelium stages as the largest flattened peripheral cells (12 by 15 μ to 14 by 18 μ in surface view; Miller, 1939, figs. 45, 46). Differentiation of the serosa is completed after all other extraembryonic cells have left the periphery and after it closes under the embryo during the invagination of the ventral plate.

During the ventral-plate stage the dorsal serosal nuclei (18 to 24 μ in diameter, 2 to 3.5 μ thick) are broader and flatter than the ventral ones (12 to 18 μ by 3.5 to 5 μ), but in the definitive serosa these differences are lost and all the nuclei are similar (20 to 30 μ by 2 to 3.5 μ), except for those of the special residual cells under the embryo. The ordinary serosal nuclei, in surface view, are round or broadly oval, with coarse chromatin granules. They number about 170 (130 to 200), and the average distance between them is calculated to be 70 to 80 μ, considering the egg as a hemisphere (actual measurements 50 to 108 μ). No mitoses occur in the extraembryonic nuclei at any time after the primary-epithelium stages. In sections of the ventral plate stage, the serosal cytoplasm is discernible only near the nuclei, and no internuclear continuity is evident. In the definitive serosa, it extends as a very thin layer (1 μ or less) between the nuclei, around the entire surface of the yolk (fig. 14; also Miller, 1939, fig. 13). Whole mounts of the serosa stained in alum hematoxylin sometimes show definite cell boundaries between many of the nuclei. The cells thus outlined are of variable polygonal form, 40 to 100 μ in diameter, and each contains a single nucleus (fig. 4).

The residual cells left under the embryo after the ventral plate invaginates are modified serosal cells and are here referred to collectively as the "grumulus" (Latin: a little heap or mound).[3] They are 20 to 30 in number and are crowded into a close group 40 to 50 μ in diameter, in the exact center of the ventral surface of the egg (Miller, 1939, fig. 7, gr). At first (stage I) the nuclei, which are ovoid, plump, and about 6 by 9 μ, are rather irregularly arranged in a copious cytoplasmic mass 12 to 24 μ

[3]This descriptive term is proposed to avoid the functional implications conveyed by the terms "hydropyle cells" and "indusium" applied to evidently homologous structures in other insect eggs, as noted later. The grumulus was tentatively called the "ventral button cells" in the original thesis and its published abstract (Miller, 1938).

high (figs. 24–27). As the grumorium, or thickening of the serosal cuticle described below, is secreted beneath them, their arrangement becomes regular and they radiate in a single layer from its convex surface (fig. 5). Finally they become flattened (12 by 6 by 3 to 4 μ), and the ragged, vacuolate cytoplasm is 5 to 12 μ thick (stage VII). The spheroid embryo is attached to the cytoplasm of the grumulus. This cytoplasmic anchor connects the caudal end of the elongating embryo with the grumulus (fig. 41) or with the neighboring serosa until stage VI, when it parts.

When blastokinesis occurs, the serosa is gathered together to form the dorsal organ (see page 445, figures 1e, 1f, and Miller, 1939, figure 14), which presumably also includes the cells of the grumulus (cf. merging of "polar organ" into the dorsal organ in the aphid *Toxoptera*, Phillips 1915). The dorsal organ is a spongy mass, approximately 185 by 90 by 50 μ, containing the degenerating, compacted remains of the serosal cells (fig. 16). It is finally engulfed in the yolk and disintegrates completely. The chromatinic remnants disappear during stage IX.

The grumulus corresponds to the cells in the grasshopper egg that have been named "hydropyle cells" (see footnote 3) by Slifer (1938a) and "the posterior serosal patch" by Roonwal (1936, 1937). In the grasshopper, the serosa in most cases breaks away from these cells and leaves them attached to the serosal cuticle when blastokinesis occurs. In *Pteronarcys*, the grumulus was never observed to persist at its original site after blastokinesis. Krause (1938, fig. 1) mentions that in the camel-cricket *Tachycines* a cushion of serosal cells ("Zellpolster") is left behind at the posterior end of the egg when the amniotic cavity closes at the anterior margin of the germ band, as the latter moves into the yolk. The association of the grumulus with the embryonic rudiment also recalls the indusium of the tettigoniid grasshopper *Xiphidium* (Wheeler, 1893) and of the homopteran *Siphanta* (Muir and Kershaw, 1912). In these species, however, the group of cells arises in front of the embryo and plays a more elaborate role in subsequent development, forming additional embryonic envelopes. The organ in the mantid *Paratenodera sinensis*, which Hagan (1917) homologized with the indusium, is much like the grumulus of *Pteronarcys*. Though nothing is said of a corresponding thickening in the so-called "vitelline membrane" (in all probability the serosal cuticle), Hagan does remark that "the organ persists in place, apparently firmly attached to the vitelline membrane, until some time after completion of revolution [not accompanied by rupture of amnion nor serosa], when it frees itself and is ingested by the embryo during the formation of the dorsal walls" (p. 227). The "polar organ" described in the winter egg of the aphid *Toxoptera graminum* by Phillips (Webster and Phillips, 1912; Phillips, 1915) is evidently also homologous with the grumulus. Here again it is a cluster of cells at the posterior pole of the egg, left behind when the cephalic end of the germ band separates from the serosa and sinks into the yolk. The germ band is tubular, one side being prospective amnion. The formation of the polar organ is thus quite similar to grumulus-formation in *Pteronarcys*, the difference lying merely in time-relations and the shape and relative position of the germ band. The aphid is even more directly

comparable to the saltatorial Orthoptera in this regard. The non-staining substance found later in the central cavity of the pear-shaped polar organ of the aphid is undoubtedly a grumorium (see below), since Phillips found ". . . that it is very difficult to remove the shell without also removing the contents of the cavity en masse, as they appear to adhere to the shell." Evidently Phillips did not pay much attention to the egg-coverings, which probably include a serosal cuticle. Leuzinger's figure 29 (Leuzinger et al, 1926) of the posterior "Zellansammlung" in the phasmid *Carausius* also suggests a grumulus, though his observation of a second similar group of cells "on the other side of the posterior pole" of some eggs does not encourage a direct comparison.

The "dorsal organ" of Collembola may also be mentioned in this connection, especially since it seems to serve, along with an associated subchorionic membrane (see below) as a sort of attachment apparatus. Wheeler (1893) homologized the indusium of *Xiphidium* with the dorsal organ ("micropyle") of the collembolan *Anurida maritima* and, further, with the dorsal organ of Crustacea and certain structures in the eggs of spiders, pentastomids, and in young and adults of leeches (*Clepsine* spp.); Willey (1899) regarded the "trophic vesicle" or dorsal organ of Onychophora as another homologue. Hirschler (1928) homologized the dorsal organ of Collembola with the primary dorsal organ of the beetle *Donacia* (also found in the weevil *Brachyrhinus:* Butt, 1936) and with certain cell aggregates in the bee *Apis* and the moth *Endromis*. The present author is inclined to regard favorably most of these opinions of probably homology and believes they may be extended to include the grumulus of *Pteronarcys* and of other species mentioned above. The subject is certainly worthy of further investigation. (See Slifer, 1938b, for similar suggestions and also for notes regarding other insects; additional remarks will be found in the conclusion of the present paper.)

"Serosal cuticle" is the term here adopted, as more appropriate than the synonymous "Blastodermhaut," for a chitinous outer membrane secreted by the serosa. It lies beneath the endochorion and encloses the entire contents of the egg. In *Pteronarcys* the secretion of the serosal cuticle begins during the ventral-plate stage. Throughout the previous younger stages the vitelline membrane is clearly distinguishable in sectioned eggs as a refringent line 0.5 μ (or less?) in thickness. It is very delicate, making it practically impossible to dechorionate a fixed egg without disrupting the contents. In the ventral-plate stage the limiting membrane, now regarded as the incipient serosal cuticle, measures 1 μ in thickness (thinner or indistinct under the germ disc) but still appears homogeneous. Though still fragile, it is already tough enough to allow the yolk to be dissected away, leaving all the peripheral cells and the ventral plate adhering to the membrane. In succeeding stages the membrane shows two distinct layers and increases in thickness to 6.5 μ, this maximum being attained by stage III. The egg contents (either fixed or living) enclosed in this tough envelope may then, with care, be removed from the chorion intact.

The definitive serosal cuticle is colorless, hyaline, and of uniform thickness on all sides of the egg. It consists of a thin, refractive outer

layer (0.5 μ) and a thick, homogeneous inner layer (6 μ) (fig. 14). The outer layer does not take light green or eosin but stains red with Mallory's connective tissue stain (orange when fuchsin is omitted); the inner layer is stained by light green and eosin and is colored blue by Mallory's stain. (This reaction to Mallory's is similar to the differentiation of exocuticle and endocuticle of the body integument by this stain.) Under the grumulus of the serosa a thick, convex "button" is secreted, 45 μ wide and 20 μ high (fig. 5). This thickening of the serosal cuticle is here termed the "grumorium" (Latin: place of, or belonging to, the grumulus or mound). Its upper portion is a thickened continuation of the inner layer of the cuticle, while its core (25 by 12 μ) seems to be a less sharply defined thickening of the outer layer, since it has similar staining reactions. The natural color of the core is yellow, which sometimes renders it visible through the chorion, and its substance is finely substriate in a radial direction. Beneath the center of the core there is sometimes a small, hyaline, lens-like thickening (fig. 5). The outer layer of the cuticle probably includes the vitelline membrane, perhaps impregnated with a toughening secretion; the inner layer seems to be secreted entirely by the serosal cells.

During stage X the inner layer shows definite signs of corrosion (fig. 15). It becomes thinner (3 to 4 μ) and its inner surface develops shallow concavities which produce a scalloped appearance in sections. This occurs long before normal hatching but undoubtedly weakens the cuticle in anticipation of that process. No further thinning takes place—a fact that may be significantly correlated with the degeneration of the pleuropodial glands after stage IX (see page 473). The serosal cuticle, ruptured by the egg-tooth at the ventral circumference when the naiad escapes from the egg (Miller, 1939, fig. 17), is left behind in the empty shell.

The serosal cuticle of *Pteronarcys* corresponds to the very similar structure described by Slifer (1937) for the grasshopper *Melanoplus differentialis*. It is formed in the same way, has two layers corresponding to the outer "yellow cuticle" and the inner "white cuticle" of the orthopteran, and suffers the same fate (though less extensively digested). The stonefly cuticle persists but weakens in cold 10% potassium hydroxide solution, weakens more in cold 5% sodium hypochlorite, and dissolves in hot 5% sodium hypochlorite; it becomes brittle in concentrated hydrochloric acid. These reactions favor the supposition that here, as in the grasshopper, at least the inner layer is of a chitinous nature; reactions of the outer layer were not studied. The inner layer is apparently more homogeneous than the grasshopper's "white cuticle" and does not attain as great thickness. Like the chorion, the serosal cuticle of *Pteronarcys* is permeable to water, since it does not prevent the contents from drying when the egg is kept out of water. It has not been determined whether this permeability is general or, as in the grasshopper egg, localized. The striate core of the grumorium evidently corresponds morphologically to the structure in the grasshopper egg which Slifer has named the "hydropyle." This is a specialized, thickened, circular area of the "yellow cuticle" showing striations and

demonstrated to be a portal for water absorption at the posterior end of the egg (Slifer, 1938a).[4]

Korschelt's (1924, p. 386–387) "secondary yolk membrane" in *Dytiscus*, secreted on the outside of the serosa, is probably homologous to the serosal cuticle. Butt's (1936) "sub-serosa" in the weevil *Brachyrhinus* differs in being formed inwardly beneath the serosa. Membranes formed in the eggs of Collembola (Wheeler, 1893; Claypole, 1898; Philiptschenko, 1912) seem to be similar to the serosal cuticle, at least in a general way. It is probable that the presence of a serosal cuticle has been overlooked in some other insect eggs or has been hidden under the misapplied term "vitelline membrane." (See also page 473.)

THE AMNION

The amnion and amniotic cavity are formed when the germ disc, or ventral plate, invaginates to form the spheroid embryo (figs. 23–25). The amnion is then represented by the ventral wall of the hollow sphere, but its columnar cells are at first indistinguishable from the potential ectoderm (fig. 25). As the embryo grows, the amniotic cavity is flattened, and the amnion becomes progressively thinner, with the cephalic portion in the lead (figs. 26–33, 36–41). Horizontal mitoses continue to occur in the amnion through stage IV. It finally becomes an extremely thin membrane with widely spaced, flat, oval nuclei 6 μ wide, 8 to 12 μ long, and 2 μ thick (one-third to one-half the size of the serosal nuclei). The amniotic fluid is not visible in sections.

The amnion is attached to (continuous with) the margin of the ectoderm and covers the entire ventral surface of the embryo. As the caudal flexure of the embryo develops (VI), the membrane spans the abdominal arch. Hence when the tail is closely flexed under the abdomen (VII), the posterior amniotic cavity within the flexure is bounded dorsally and ventrally by the germ band and only laterally by the amnion; i. e., the amnion is not folded within the flexure (figs. 1b-1d, p. 445). After blastokinesis (p. 445) the amnion encloses the yolk dorsally (VIII) (figs. 1e, 1f). It is gradually incorporated into the dorsal organ (fig. 16) as the body wall grows dorsally and replaces it; and it finally degenerates in the yolk.

THE ENTAL MEMBRANE

"Ental membrane" is a new term here proposed to designate a very thin membrane extending over the upper surface of the germ band and separating it from the yolk, in a manner not unlike the ventral amnion (figs. 1a-1f; *em*).[5] This structure appears to be homologous with that

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[4]Although the description of the grumorium stands as written before Slifer's paper came to hand, it shows striking similarity to her description of the hydropyle (making due allowance for differences in the general form of the structures). In both stonefly and grasshopper, the inner cuticle is continuous over the striated outer layer. The inner cuticle of the grasshopper egg, however, is thinner at the hydropyle than elsewhere.

[5]The term "entamnion" (Greek: *ento*, inner, + *amnion*), mentioned in the previous paper (Miller, 1939, p. 578), would be a shorter alternative for "ental membrane." The original intention was to indicate merely an amnion-like mem-

described by Roonwal (1937) in *Locusta migratoria* and called by him "the provisional dorsal closure," a term that is more cumbersome and less appropriate for the structure in *Pteronarcys*.

When fully developed (e. g., in stage VII), the membrane appears in section as a fine line, less than 0.5 μ (0.2 μ?) thick, extending over the entire upper surface of the embryo and forming an intact boundary to the yolk (fig. 20). Its study requires the use of the oil-immersion objective. (Seeming discontinuities in the membrane are probably not real: even the membranous portions of the amnion are frequently invisible, though their presence is indicated by the aligned distribution of widely spaced nuclei and by the sharp boundary between yolk and amniotic cavity where no membrane is apparent.) The ental membrane is attached to the ectoderm at a point just above the origin of the amnion (fig. 18). Scattered throughout its extent, both laterally and medially, there are small isolated cells, either incorporated in the membrane itself or attached to its ventral surface (fig. 19). These cells, when fully differentiated, are characterized by a diffuse nucleus and large vacuoles, with the cytoplasm forming thin radiating partitions and a delicate peripheral layer. The cells are ovoid or spheroid in form, 5 to 8 μ in diameter. The membrane is attached to their peripheries and probably represents extensions, or a product, of their cytoplasm. Such cells and the associated membrane are present around and under both proctodaeum and stomodaeum, though the main portion of the membrane extends between the ventral margins of these two invaginations. The membrane also closes the gap between the dorsocaudal margin of the head and the stomodaeum, and (later) between the anterior margin of the dorsally-closed abdominal segments and the tip of the proctodaeum (figs. 1c-1e, p. 445).

The mode of origin of the ental membrane is not clear (see below). Cells which may be young membrane cells are sometimes apparent in the protocephalon and gnathal segments as early as stage IV, soon after the beginning of segmentation and while the protocephalon is still broad and flat. But interpretation is rendered uncertain by the spreading of the protocephalic mesoderm at this time and by the lack of definite evidence as to the origin of the observed cells. However, the membrane cells become clearly recognizable in late stage IV and early V, when they appear as isolated cells in the protocephalic and gnathal region (fig. 45: *emc*). They are few in number, usually widely separated, and fusiform in section. Each consists of a dense, flattened nucleus (4.5 by 2, to 10 by 3 μ) surrounded by a very thin layer of cytoplasm which tapers off peripherally (fig. 17). An extremely delicate membrane is occasionally detectable in association with these cells or spanning irregularities of the underlying tissues (e. g., from crest to crest of coelomic sacs). It presumably covers the entire dorsal surface of the embryo, but its delicacy would render it invisible where directly applied to the tissues. It seems to pass over the tip of the stomodaeal invag-

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brane covering the ental surface of the embryo, in contrast to the true ectal amnion. "Entamnion", however, may carry the unwarranted implication that the structure is directly associated with the true amnion, and it seems advisable to discard the term and to use instead only the unambiguous designation, "ental membrane."

ination. Though the membrane is present in the abdomen before the proctodaeal invagination begins, it is not until the latter has deepened considerably (60 μ, in stage VI) that the membrane is detectably associated with it in the preparations at hand. At this stage the membrane extends forward from the tapering ventral margin of the tip of the proctodaeum, and membrane cells are present between the proctodaeal mesoderm and the underlying segmental mesoderm. As the protocephalic lobes curl up and the caudal abdominal segments close dorsally, the membrane and its cells (which gradually assume their definitive character) are clearly seen as an inner lining in these regions, as well as over the entire area between stomodaeum and proctodaeum.

After blastokinesis, the ental membrane is drawn over the sides and, eventually, the dorsum (relative to the embryo) of the yolk by the advancing edge of the body wall. Yolk and embryo are separated by a membrane that is interpreted as being either identical with or inclusive of the ental membrane. The latter thus forms a provisional bounding membrane for the incipient mid-gut and further serves as a surface over which the true mid-gut cells spread. This spreading takes place over the yolk-side of the membrane, while the splanchnic mesodern spreads beneath the membrane. Occasional membrane cells are recognizable (though usually flattened) around the yolk as late as stage IX. They probably eventually degenerate. Pyconic degeneration products are sometimes evident in appropriate positions, but their identity is uncertain. Such chromatinic spots also occur very commonly (stage VIII) in and around the caudal fat body, less commonly in the head region; they possibly represent or include the membrane cells in these areas. A group of typical membrane cells persists beneath the tip of the stomodaeum through stage IX, but their fate was not determined. Increasing numbers of young blood cells which resemble the membrane cells confuse interpretation in these later stages. The use of the ental membrane as a basis for the dorsal diaphragm would be entirely possible caudally, but no conclusive evidence can be offered in this regard.

Assuming the membrane to be attached to the marginal ectoderm throughout its extent, as the evidence indicates, its subsequent distribution is affected by the growth of the embryo probably in the manner shown in the accompanying diagrams (text fig. 1). This scheme would explain the presence of membrane cells around the sides of the stomodaeum and proctodaeum, though the doubleness of the membrane beneath the latter is not directly demonstrable, perhaps owing to its delicacy. Nor can the membrane be detected covering the tip of the proctodaeum. However, degeneration products appearing in the yolk nearby suggest that the lengthening proctodaeum pushes through such a layer and causes necrosis of the membrane cells at that point. It is of interest to note that, with this exception, occasional (mesodermal) paracytes are found in the yolk above the embryo only before, and not after, the ental membrane becomes evident. (Roonwal, 1937, attributes the absence of paracytes in *Locusta* to the presence of the similar membrane in that insect.)

Despite considerable effort to determine the origin of the ental

membrane cells, the material studied failed to reveal how or whence they arise. It seems most probable that the cells arise either from the lateral ectoderm, not far above the line of attachment of the amnion, or somewhere from the mesoderm, both protocephalic and protocormic. Whatever their origin, the cells probably produce the interconnecting membrane. Neither an ectodermal nor a mesodermal origin of the cells has been demonstrated as yet. There is no evidence that the ental membrane is to be associated with the early yolk-cell membrane reported in *Locusta* by Roonwal (1936) and in *Carausius* by Leuzinger and Wiesmann (Leuzinger et al, 1926), nor with the secondary nuclear aggregates or other yolk cells in *Pteronarcys* (p. 449).

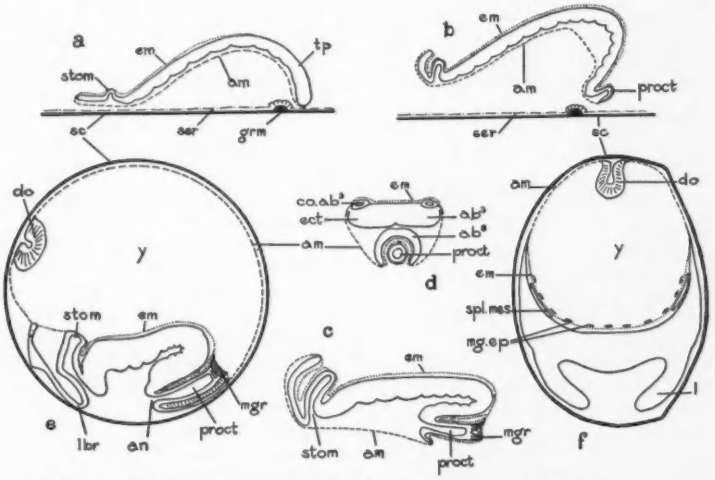

Fig. 1. Diagrams illustrating the relative positions of the embryonic membranes during various stages of development of *Pteronarcys proteus*. In the anterior and posterior regions, the distribution shown for the ental membrane is partly hypothetical (see text). No fixed scale; *a-d*, before blastokinesis; *e*, *f*, after blastokinesis; *a*, *b*, *c*, *e*, sagittal sections, *d*, *f*, transverse sections of embryo. For abbreviations, see page 471.

The observations tending to favor a lateral-ectodermal origin are as follows: The membrane is evidently always connected to the marginal ectoderm of the germ band; isolated cells which are probably membrane cells appear early above the protocephalic ectoderm where no mesoderm is present; occasional early isolated cells occur above intact coelomic sacs which give no indication of having produced the cells, thus suggesting an inward migration from the lateral ectoderm; the probably homologous membrane in grasshoppers, discussed further on, appears to arise from the marginal ectoderm; a general analogy with the amnion might suggest that the ental membrane is likewise ectodermal, though such a view is *a priori* and unjustifiable. None of these observations is

conclusive, for the isolated cells in all probability migrate, so that their observed position gives no direct indication of their place of origin. The strongest argument, coupled with the evidence from grasshopper embryos, is provided by the definite connection of the ental membrane to the marginal ectoderm, sometimes visible even in early stages. Unfortunately, the material at hand does not show unmistakable evidence of lateral proliferation of the membrane cells, though suggestive images are sometimes found (lateral ectodermal mitoses or flattened dorsal nuclei near the edge). If the cells do arise laterally, they must migrate mesad, forming the membrane as they go.

On the other hand, certain observations tend to favor the possibility of a mesodermal origin for the ental membrane cells: The cells sometimes are more apparent medially than elsewhere in early stages; occasionally the proximity of a medial cell to a coelomic sac is suggestive of a possible origin therefrom; the membrane is evidently continuous across the mid-line in later stages; the membrane appears as a direct extension of the ventral apex of the mesoderm surrounding the proctodaeum; the fully differentiated cells look much like blood cells; the cells of a possibly homologous membrane in the stick-insect *Carausius* have been described as arising from extensions of the coelomic sacs (see below). Again, the observed position of the cells may signify nothing as to their origin; no direct proliferation of cells from the coelomic sacs has been observed and both cells and membrane are present and extend over the sacs before the latter break down; and a medial origin would require that the membrane become secondarily connected to the lateral ectoderm. Here the strongest evidence is the apparent similarity of the ental membrane to the membrane in *Carausius*, definitely described by Leuzinger and Wiesmann (1926) as formed by cells originating in the "blood-cell plates" (Blutzellenlamellen or Blutzellenmembranen) which are rostromedial extensions of the coelomic sacs, and hence mesodermal. According to these authors, the migrating cells draw a thin cytoplasmic layer behind them which fuses with and eventually replaces the overlying "yolk cell membrane" (interpreted as primary endoderm) and so form a secondary endoderm which becomes the mid-gut epithelium. This replacement progresses laterad from the median line. No mention is made of a connection to the marginal ectoderm. Resemblance to the ental membrane of *Pteronarcys* is limited to the general appearance of cells and membrane, as described and figured by Leuzinger and Wiesmann; the role of the structure in *Pteronarcys* is regarded as temporary rather than definitive.

A comparison with Roonwal's "provisional dorsal closure" in *Locusta* shows a close correspondence to the ental membrane of *Pteronarcys* up to the time of blastokinesis. After blastokinesis, however, the membrane in *Locusta* is said to tear away from its primary connection with the lateral ectoderm, the free edge thus formed spreading over the sides and top of the yolk independently of the body wall. The space between the (everted) amnion and this provisional dorsal closure forms a lateral blood sinus on each side. The dorsal membrane is later replaced by splanchnic mesoderm and degenerates. The ventral portion of the membrane separates yolk and epineural sinus just as it does in *Pteronarcys*, though in the latter the epineural sinus is still

potential or greatly compressed. A condition similar to that in *Locusta* is also figured for *Stenobothrus* (another acridid) by Graber (1889). He diagrams the membrane in his text figure 13 as arising by ingrowth from near the juncture of amnion and ectoderm on each side, the two halves finally fusing dorsally on the mid-line. His plate figure (pl. I, fig. 1) shows an intact ventral amnion at this time and yolk both above and below the membrane, but with somatic and splanchnic mesoderm interposed between the membrane and the inner yolk. The condition in *Stenobothrus* requires further investigation. Roonwal did not determine the genesis of the provisional dorsal closure in *Locusta* but (like Graber) considers it ectodermal in nature, evidently because of its connection with the lateral ectoderm. Evidently the "mesenteron rudiment" or "entodermal membrane" in *Melanoplus* mentioned and figured by Nelsen (1934) is the same structure as Roonwal's provisional dorsal closure; Nelsen states that it arises from inner-layer cells "associated with the internal lips of the stomodaeum and proctodaeum," but he gives no supporting evidence.

While the cited works of Graber, Roonwal, Nelsen, and Leuzinger and Wiesmann constitute the only other records of the ental type of embryonic membrane known to the author, it seems likely that search for similar structures in other insects, particularly Exopterygota, would prove fruitful. Evidently the membrane is more conspicuous in acridids than in *Pteronarcys*, as a result of the larger size of the early epineural sinus and perhaps also of the embryo and the membrane elements as a whole. A delicate membrane closely applied to the upper surface of the embryo could easily be overlooked and the membrane cells mistaken for median blood cells or other types of cells (e. g., Strindberg's "endoderm cells" in the termite). Such a practical, though provisional, structure might well be of general use in forms having a slow mid-gut development.

THE EMBRYONIC CUTICLE AND EGG-TOOTH

During stage VIII-IX there is secreted by the hypodermis of the embryo a thin cuticle or pellicle, specialized on the front of the head to form an egg-tooth. This embryonic cuticle and egg-tooth are cast off when the insect hatches, the definitive cuticula having been formed beneath them during stage X. The embryonic cuticle is, of course, entirely distinct from the serosal cuticle.

The embryonic cuticle is presumably secreted over the entire surface of the body and of the individual appendages, and also in the lumina of the stomodaeum and proctodaeum (fig. 22). It is thus a direct product of the ectoderm (hypodermis and epithelium of fore- and hind-guts). It covers the tips of the tarsal claws individually but at their base surrounds the pair of claws as an undivided sheath. It does not cover the pleuropodial tufts (fig. 11). Though the continuity of the cuticle is difficult to detect with certainty in sections of late stages when the definitive cuticula has been formed, it has been observed as a filmy, transparent pellicle closely ensheathing the abdomen (setae appressed beneath it), head, and appendages in living embryos removed from eggs and also, fragmentarily, immediately after hatching. The pellicle is extremely delicate and is apparently rubbed off piecemeal during

hatching; only the robust egg-tooth retains its forms after it is shed. It is possible that pleuropodial or other secretions may have a dissolving action on this pellicle as well as on the serosal cuticle.

In sections of stage IX the embryonic cuticle is 0.5 to 0.8 μ thick (fig. 22). The definitive cuticle, later secreted beneath it, attains a thickness of about 4 μ.

On the front of the head the embryonic cuticle is thickened to form a plaque on which is situated the egg-tooth (figs. 21, 22). This tooth and about 30 filiform or clavate excrescences on the lower end of the plaque, above the labrum, are the sole outgrowths of the embryonic cuticle; no setae are present. The hypodermal cells that are to secrete the egg-tooth show some enlargement in stage VII, but become fully differentiated in stage VIII after blastokinesis. These frontal cells at this time form a conical swelling, with the central cells 15 μ high while the neighboring unmodified hypodermal cells are only 4.5 μ high. The egg-tooth is secreted over the surface of the enlarged cells, which thereupon decrease in height and exhibit some degenerative nuclear changes (stage IX, fig. 22). The sclerotized egg-tooth thus formed is conical and hollow, its rather blunt, dark tip formed by the central convergence of four hard ridges (fig. 21). Basally it merges into the thickened plaque or foot-plate which covers the fronto-clypeal region of the head, while the tooth proper is between the arms of the epicranial suture (Miller, 1939, figs. 15, 16b). The plaque attains a thickness of nearly 5 μ, tapering off into the thin embryonic cuticle at its margins (fig. 22); in stage X it is underlaid by the definitive cuticula (4 μ thick). The reticulations shown in the surface view of the plaque (fig. 21) are presumably molded by the hypodermal cells or the rugulose definitive cuticula.

As the embryo assumes its prehatching position in stage X, the egg-tooth is directed against the serosal cuticle in the angle where the dome and floor of the egg join (cf. Miller, 1939, figs. 1, 16b). Since the plaque is loosely attached to the head, the tooth probably performs its hatching function merely as a wedge forced against this weak point of the shell by outward pressure of the head. The serosal cuticle and shell split open around the perimeter of the floor, and the naiad pushes its way out as illustrated in the previous paper (Miller, 1939, fig. 17), sloughing off the egg-tooth and pellicle in the act of hatching.

According to the compilation by van Emden (1925) and individual observations by other authors (Wheeler, 1889; Muir and Kershaw, 1912; Hagan, 1917; Smith, 1920, 1922; Carothers, 1923; Heymons, 1926; Sikes and Wigglesworth, 1931), an embryonic cuticle is found in Orthoptera, Mantoidea, Dermaptera, Odonata, Corrodentia, Heteroptera, Homoptera, Anoplura, Mallophaga (exopterygotes), and in Neuroptera, Trichoptera, and a few Coleoptera (endopterygotes). It also occurs in Araneida, Diplopoda, and Chilopoda. It is said to be absent in Thysanura. Among the Endopterygota (Holometabola), it is absent in Diptera and Siphonaptera and has evidently not been reported for Lepidoptera, Hymenoptera, and most Coleoptera. An unpaired cephalic egg-tooth on the embryonic cuticle (cast off at hatching) occurs in Opiliones, Diplopoda, Orthoptera, Mantoidea (plaque only), Dermap-

tera, Odonata, Corrodentia, Heteroptera, Homoptera, Neuroptera, and Trichoptera, while a persistent egg-tooth on the definitive cuticula (retained by the first instar) occurs in Lepisma and the larvae of eucephalous Diptera, Siphonaptera, and a few Coleoptera. (Paired cephalic, buccal, and thoraco-abdominal hatching spines also occur in some insects and other arthropods: see van Emden, and Sikes and Wigglesworth.) Van Emden homologizes the embryonic cuticle with the first larval cuticula of Holometabola; Heymons (1926) regards egg-teeth in such widely different insects as the result of convergent evolution and hence not necessarily homologous *inter se*.

THE YOLK AND YOLK CELLS

The yolk at successive stages of development contains several types of cells, viz., the cleavage cells, nuclear aggregates ("primary," before, and "secondary," after differentiation of the germ disc), vitellophags, and degenerating paracytes. More than one type are present simultaneously in the earlier stages, but finally the vitellophags alone remain. The cleavage cells and early nuclear aggregates have already been described (Miller, 1939). After cleavage the number of discrete cellular elements in the yolk decreases markedly; later, when growth of the embryo begins, it increases to its maximum.

The *nuclear aggregates* which occur in the ventral-plate stage may be called "secondary" in contradistinction to the "primary" presumptive embryonic clumps of earlier stages. The secondary aggregates are often obviously imbedded in cytoplasm connected with the germ disc (Miller, 1939, fig. 50); they are presumably derived from the ventral mass during rearrangement of its cells to form the disc. Plump single and compound nuclei, without evident cytoplasm, also occur in the surrounding ventral yolk and may represent nuclei left out of the ventral mass or aggregates that have wandered laterad. These various elements number between 10 and 20 and range in size from 8 by 14 to 14 by 18 μ. The compound nuclei consist of 2 to 7 (occasionally perhaps more) components, the smaller groups predominating; where component nuclei are distinct, they measure 6 by 6 to 5 by 9 μ. In the spheroid stage (I), they may be widely distributed in the yolk, but there are almost always a few (up to four) large single or compound nuclei near the spheroid embryo, sometimes applied to its dorsal surface (figs. 23, 25, 27). (The latter, which are held over from the ventral plate stage, suggest a possible homology with the yolk-cell membrane described in *Carausius* and *Locusta* (Leuzinger et al, 1926; Roonwal, 1936), but no actual membrane is formed. They seem to arise from the embryonic rudiment in *Pteronarcys*, and like the yolk cell membrane—which also arises from the germ band in the other species—could be regarded as representing primary endoderm.) The secondary aggregates and large nuclei disappear in later stages. Some are still detectable in a late stage-II egg, but they are distorted or attenuated and appear to be pulling apart (fig. 3b). Thereafter only single nuclei occur in the yolk. This suggests that they probably form secondary vitellophags that become indistinguishable from those derived directly from the primary epithelium, especially since no signs of degeneration occur in the aggregates.

The *vitellophags* are supposed to consist entirely of the secondary type, derived directly or indirectly from the primary epithelium. Primary vitellophags which arise by direct metamorphosis of cleavage cells are presumably absent, though this is difficult to prove (see Miller, 1939, page 588). The majority of the secondary vitellophags are represented in the late primary epithelium as flattened nuclei that are smaller than the pre-serosal nuclei, measuring 7 by 7 to 7 by 11 μ, and 1 to 2 μ thick. Though a few may sink into the yolk earlier, most of them are drawn in during the centripetal aggregation of prospective embryonic cells, when they are found just under the periphery and still retain their flat form (Miller, 1939, figs. 45, 46). Thereafter they become distributed throughout the yolk and more or less distorted, so that all shapes are found, though traces of the laminate character persist (fig. 3a). The nuclei are dark-staining, have coarse chromatin granules, and sometimes show traces of sparse, irregular cytoplasm surrounding them. They vary greatly from compact ovoid forms 7 μ in diameter to thin, irregular individuals 12 μ or more in largest dimension. Probably their shape is changeable during life. The number of yolk nuclei increases from the ventral plate stage (e. g., 94 single and compound nuclei) to as many as 300 during the spheroid stage. This indicates continued inward migration from the periphery and is correlated with a decrease in the number of peripheral nuclei from about 300 to about 170 (the definitive number of serosal nuclei). After the secondary aggregates separate to form vitellophags, the latter probably remain constant in number (200 to 300). (With the exception of the cleavage cells, no mitoses ever occur in yolk nuclei.)

The *paracytes* are degenerate embryonic (as opposed to extra-embryonic) nuclear material which appears in the yolk in the form of small dark-staining clumps or globules of chromatin. The term is here used in a broad sense and is not limited to mesodermal elements. Similar pycnotic clumps may occur within the embryonic tissue itself and in many cases undoubtedly represent paracytes which are later cast into the yolk. Mention has already been made (Miller, 1939) of such degeneration products among the prospective embryonic cells during ventral streaming, in the ventral mass and ventral plate, and in the yolk during these latter stages (cf. figs. 47 to 52 in the earlier paper). Those in the yolk are presumably degenerate cells left out or expelled from the embryonic tissue as the ventral mass and plate are formed. Degeneration products are still abundant in—especially ventrally and near the outer surface—and around the spheroid embryo (I), but they soon become fewer and disappear (figs. 25, 26; cf. also figs. 23, 24). Thereafter they are relatively rare. They are found in the anterior and caudal cells of the elongating embryo (fig. 33) and occasionally in the yolk above the median line of the embryo before the ental membrane is formed, usually near a region that is bending during growth. In later stages a few occur near and in the tip of the proctodaeum. In all cases their presence could be attributed to necrosis induced by intraembryonic compression or growth pressure against surrounding constituents of the egg. Perhaps such factors are really involved in their production.

Very definite *yolk cleavage* occurs during stage II and is evident in some preparations as late as stage X. Evidently the condition is often obliterated by fixation; it shows best in material fixed with Schaudinn's fluid, is often apparent after fixation with Dietrich's fluid, but is obscure or absent in eggs fixed in alcoholic Bouin's, Zenker's, and Petrunkevitch's fluids. Up to the time of this cleavage, the fixed yolk retains the appearance, found in the newly-laid egg, of a dense mass of irregular granule-like yolk bodies, usually 10 μ (but up to 21 μ) in diameter, interspersed with spherical oil vacuoles (see Miller, 1939). There is some indication that the oil globules increase in size as yolk cleavage approaches, one stage-II egg showing negative images as large as 50 μ in diameter. In yolk cleavage the entire yolk becomes divided into polyhedral masses 50 to 100 μ in diameter, each apparently with a single, flat vitellophag (12 by 1 μ) in its center (fig. 34). Each mass (when fixed) consists of a homogeneous matrix containing medium-sized oil vacuoles between which run fine fissures (probably artifacts). The fissures tend to divide the polyhedron into fragments corresponding to the original yolk bodies; this, when carried far enough under the influence of certain fixatives, obliterates the yolk cleavage entirely. Yolk cleavage unquestionably occurs in life, since it has been observed in the transparent living eggs of other insects (e. g., by Seidel, 1929; Roonwal, 1936; Krause, 1938). Perhaps it involves merely a physico-chemical change in the emulsion constituting the yolk, as a result of an increase in digestion products adding a third phase to the fat-protein emulsion. If cytoplasm is instrumental in delimiting the polyhedra, it is invisible.

That the vitellophags are really involved in *yolk-digestion* is suggested by their occasional, though infrequent, association with certain small, grayish, translucent globules (fig. 3c, d). These have been observed in material fixed with Dietrich's or alcoholic Bouin's fluid and stained with alum hematoxylin alone, or fixed with Petrunkevitch's fluid and stained with iron hematoxylin. The spheres are 6 to 12 μ in diameter and are almost always found in contact with a vitellophag nucleus, usually singly but also in twos or threes; they are rarely isolated. (Apparently similar spheres were observed in *Eutermes* by Strindberg, 1913, p. 164.) During stage X the yolk begins to appear "liquified" in sections, the yolk bodies decreasing in number and a coagulum appearing among them. In the non-feeding postembryonic instar, the mid-gut is filled with this coagulum and the yolk bodies disappear completely. These appearances may reflect an increased fluidity of the yolk, which is really liquid in character (a sol) from the beginning, but it is also likely that the coagulum is an accumulation of excretory wastes.

The fate of the vitellophags is of particular interest. It is certain that many of them simply degenerate when development within the egg is complete; perhaps all of them do. The degenerative changes can be followed and their pycnotic remains are seen in the mid-gut contents of stage X and of the hatchling. It is uncertain whether or not vitellophags are also responsible for the formation of the mid-gut lining-membrane that is present in the first instar naiad, a structure that will be described in a later paper.

Morphogenesis

CHANGE IN FORM AND POSITION

The invagination of the discoid ventral plate to form the spheroid embryo (cf. Miller, 1939, figs. 6, 7) probably occurs rather quickly. Though both plates and spheres were found in sib eggs fixed simultaneously, intermediate stages were rarely encountered. That invagination does occur is indicated by the relative sizes of the plate and sphere (Miller, 1939, p. 576). (Analogous processes occur in other insects during formation of the amnion: see page 442). The embryos illustrated in figures 23 and 24 are two of four that seem to represent the process of invagination. In figure 23 the ventral plate has buckled up and the edges are beginning to turn under; in figure 24 the edges have come together ventrally. Compaction follows and the spheroid embryo then appears as in figure 25; the ventral wall is prospective amnion while the dorsal portion is the embryo proper (*ect*). The fragments enclosed in the incipient amniotic cavity appear to be bits of cytoplasm; they finally disappear completely (fig. 26). There is some indication that this invagination is essentially asymmetric and that the residual serosal cells forming the grumulus arise (mainly?) at one edge of the germ disc, rather than from cells along its entire periphery. The grumulus is invariably toward one side of the sphere and never directly beneath it (fig. 25). The general appearance of the embryo in figure 23 also suggests this conception, which might further regard the amnion as being preponderantly of cephalic origin, considering the polarity of the embryo that later becomes evident.

The elongation of the embryo involves not only mitoses but also changes in the shape and probably position of cells, especially during the flattening of the sphere (cf. dimensions given in Miller, 1939, p. 576–578). The mitoses are scattered throughout the embryo so that caudal growth is not solely the result of local proliferation (at least through stage III). As the protocephalic lobes increase in size (II–IV), they become thinner than the protocorm; the latter, with its inner layer, remains thick and subcylindrical (figs. 28–33). As the embryo lengthens, its anterior end moves toward the side of the egg, while its caudal end remains associated with the grumulus, lying either on it or to one side (Miller, 1939, figs. 8–11). This caudal attachment is perhaps instrumental in bringing about the dorsal arching of the embryo, though the arching may become manifest before the anterior end reaches the side of the egg. In stages IV and V, direct contact between embryo and grumulus may be lost, but the caudal end remains attached to the serosa by a cytoplasmic connection (fig. 41) which is finally severed in stage VI. Elongation also pushes the protocephalon dorsally along the side of the egg (IV) and is probably responsible for the lateral buckling of the slender embryo when it attains its maximum length (V–VI) prior to broadening and shortening (VI–VII). As the protocephalon moves dorsally and its lobes begin to turn up, the anterior amnion is finally withdrawn from the serosa. This allows the yolk to penetrate between the two membranes anteriorly, just as the arching of the embryo had previously enabled the yolk to close under the embryo ventrally. Since both cephalic and caudal ends part from the serosa, the

embryo becomes completely immersed in the yolk (VI–VII; Miller, 1939, figs. 12, 13). The arching of the abdomen resolves itself into a typical caudal flexure, so common in insect embryos.

After the shortening which accompanies consolidation of the body regions, further growth necessitates a change in the position of the embryo. This is accomplished by blastokinesis. (The process itself was not observed, and no intermediate stages between VII and VIII are represented in material studied.) Prior to this, contact between the cephalic amnion and serosa is re-established, and they adhere firmly, judging by fixed material. The embryo changes from its immersed, transverse, and horizontal position (VII; Miller, 1939, fig. 13) to a position in which it lies on its right (rarely left) side with its ventral surface against the lateral wall of the egg, i. e., on one side of the yolk (VIII; fig. 1e, and Miller, 1939, fig. 14). The yolk mass, filling one-third of the egg, is now enclosed in the reflected amnion, while the serosa has been gathered into a compact mass (the dorsal organ) at a point on the circumference of the egg not far from the embryo's head. Blastokinesis, then, must involve the rupture of the fused amnion and serosa in front of the head, as it does in many other insects. The embryo slips out of the amniotic sac and out of the yolk through this rent in the membranes, at the same time turning on its side. The serosa contracts and the amnion turns inside out as it is stripped caudally from the embryo's venter, to be dorsally reflected over the yolk. In the yolk sac thus formed, the formerly outer surface of the amnion becomes innermost, still retaining its contact with the yolk. The position of the embryo relative to a given side of the egg before and after blastokinesis was not determined, because the egg bears no distinctive fixed features at any point of the circumference. However, the process must involve almost complete end-for-end reversal of the embryo; the everted embryo extends over one-third the egg's circumference, with its tail probably in the region occupied by the head while immersed, and its head at a point adjacent to the former position of the tail.

Blastokinesis is probably facilitated by the presence of fluid between the serosa and the serosal cuticle.[6] This fluid, which appears as a turbid coagulum in sections, accumulates from stage III onward, becoming greatly augmented and concentrated near the head end of the embryo just before blastokinesis. After blastokinesis it surrounds the appendages of the embryo, and in stage IX penetrates into the stomodaeum and proctodaeum. The fluid may consist largely of waste products given off during development, diffusible through the serosa but not through the serosal cuticle. It is stained by plasma stains (eosin, light green), shows at most a faint lilac tinge with alum hematoxylin, and does not retain iron hematoxylin until stage X, when little remains outside the embryo. The invisible true amniotic fluid must be added to the extraserosal fluid when blastokinesis occurs. According to Sikes and Wigglesworth (1931), insects commonly swallow the "amniotic fluid" just before hatching; perhaps *Pteronarcys* does the same to this "peri-embryonic fluid."

[6]Liquid between serosa and cuticle is also noted in the grasshopper egg by Slifer (1937), who states that it is coagulated by alcohol and precipitated by heat or distilled water, gives a positive biuret reaction, and has a pH of about 6.2.

The method by which the cephalic rupture of amnion and serosa during blastokinesis is effected is not known. It seems probable that enzymatic action may be involved, but if such enzymes exist, it is entirely speculative whether they are of purely local origin (note proximity of the prospective egg-tooth-forming cells) or are added to the amniotic fluid from more remote sources and encounter necessary complements for activity only at the point where amnion and serosa are in contact. It is not known whether the pleuropodial glands are already active at this time (stage VII); they have not yet reached their full development (see page 460 and figure 9).

Blastokinesis must be regarded as a mechanical necessity in this species. Whereas the length of the immersed embryo would be limited by the diameter of the egg, the change in position puts the entire circumference at its disposal for expansion. Blastokinesis simultaneously enables an appropriate shift of the yolk preparatory to its enclosure within the gut of the embryo.

Change in position after blastokinesis (stages IX and X; Miller, 1939, figs. 15, 16) is the natural result of dorsal closure and increase in length. Dorsal closure is already complete in the head and well along in abdominal segments 8–11 (where no yolk is present) before blastokinesis occurs. Thereafter, with dorsal growth of the body wall, it progresses centrally and encloses all the yolk within the embryo.

FORMATION OF THE INNER LAYER

The inner layer, which seems to represent mesoderm only, first appears during stage I. It is not recognizable in the ventral plate and invagination stages, nor in early spheroid embryos (figs. 23–25). Later spheroid and ovoid embryos, however, and the pyriform stage II, show a median double-layered condition in the dorsocaudal region, where a small group of polyhedral cells lies on top of the ectoderm (figs. 26, 27). This is the beginning of the inner layer. It probably arises by a shift of one or more cells dorsally from the ectoderm. Direct proliferation from the ectoderm is also a possibility, but if it occurs, it is probably limited to the early stages. Despite an abundance of mitotic figures in all parts of the elongating embryo (including the mesoderm itself), none are so situated as to suggest later additions to the inner layer by this means (fig. 33). No indications of a gastrular furrow are detectable at any time. There is neither evidence nor likelihood that the neighboring yolk cells are involved in the formation of the inner layer.

In stages II and III, the elongating inner layer is more or less convex dorsally, especially caudad, and extends from the base of the protocephalon to the posterior end of the embryo (fig. 33; Miller, 1939, figs. 8, 9). In the protocorm it may be somewhat compressed by lateral upgrowth of the ectoderm, which in cross-section appears as a trough in which the mesoderm lies (figs. 5, 29, 31, 32). The median ectodermal cells are more or less compressed as a result of this concavity and sometimes present what is probably a false appearance of pushing upward into the mesoderm. Since the inner layer is sharply demarcated from the ectoderm throughout the length of the protocorm (fig. 33), it is believed that no additions from below occur in this region, but that the inner layer keeps pace with the growth of the embryo by intrinsic

cell-division. Compressed cells at the anterior end of the inner layer in the protocephalon of the slipper-shaped embryo (II) suggest additions to the mesoderm at this point (fig. 28), but it is an open question whether actual shifting of cells from one layer to the other does occur in this stage. The anterior demarcation between the layers is more definite in stage III (fig. 30).

According to the review given by Roonwal (1936), the inner layer is formed in Orthoptera either by invagination (proliferation from the roof of a mid-ventral groove) as in Acrididae, Tettigoniidae, and Mantidae, or by immigration (proliferation diffuse—all over the germ band; or localized—mostly from special lateral areas of the germ band) as in Phasmidae; or by both these methods, as in Blattidae and Gryllidae. In Dermaptera the inner layer arises by localized immigration, in Isoptera (Knower, 1900; Strindberg, 1913) by diffuse immigration. Inner-layer formation in *Pteronarcys* must be classified as of the localized immigration type.

SEGMENTATION AND FORMATION OF COELOMIC SACS

The data at hand regarding the sequence of segmentation, formation of coelomic sacs and initial appearance of appendage buds are summarized in the accompanying chart (fig. 2).

The first regional differentiation occurring in the germ band is that which marks off protocephalon from protocorm, the former increasing in width and decreasing in thickness, the latter remaining narrow and becoming progressively longer (stages II and III; Miller, 1939, p. 577 and figs. 8, 9). Segmentation begins in the protocorm during stage IV, but the exact sequence of this initial segmentation is not evident in the material studied (see below). As indicated in the chart, the segmentation becomes definitely analyzable only after the gnathal and thoracic segments have become demarcated. Thereafter (at least), segments are added posteriorly as the embryo lengthens. From the beginning, however, there is considerable lag between caudal extension and segmentation, so that throughout stages IV and V an unsegmented "tail-piece" is present behind the segmented region (figs. 36, 38; Miller, 1939, fig. 10). Segments are progressively differentiated from the anterior portion of the tail piece by constrictions that appear in the ectoderm earlier than in the mesoderm. The proctodaeal invagination begins before the last four abdominal segments are distinct (fig. 41), and differentiation of the cerci is also precocious. The last (eleventh) embryonic abdominal segment is represented by only a short rim around the proctodaeal orifice, bearing the cerci laterally. A telson or periproct cannot be recognized as a separate structure distinct from this last segment.

The chart in figure 2 and general appearances suggest that in stage III the embryo consists only of protocephalon and the presumptive gnathal region, the thorax and abdomen having still to be added by caudal growth. There is, however, no assurance that this is true as far as the presumptive significance of the existing protocorm is concerned: thoracic and abdominal building material is probably present, at least at the extreme caudal end and even perhaps more anteriorly. The identity of the earliest suggested segments (chart, embryos Nos. 2–5)

has not been determined with certainty. Interpretation of the pertinent material is rendered doubtful by unfavorable planes of sectioning, and no conclusive evidence has been obtained by examination of whole mounts. Mere relative position of the poorly defined early segments is inadequate as a criterion of identity. While, for example, the third segment may seem to correspond to the second maxillary segment of older embryos, this is not necessarily true. Interpolation of more anterior segments by subdivision of the earliest "segments" is a possibility not to be disregarded. This uncertainty concerning early segmentation in the gnathal and thoracic regions leaves undetermined two important questions, viz., whether prosegments are formed and later subdivided, and whether the visible differentiation center is truly cephalic or (as in many insects—see Richards and Miller, 1937) prothoracic. If prosegments do occur, they need not, of course, correspond to the definitive tagmata. There is no indication that the latter develop as primary divisions of the germ band, but rather by later grouping of segments as shown in the chart. The critical import of the sequence of gnatho-thoracic segmentation in regard to the differentiation center prompts cautious interpretation of early events in that region of the protocorm. However, after four or more segments are well demarcated in the ectoderm (chart, embryo No. 6) and coelomic cavities appear (embryos Nos. 7 and 8), there is less reason to mistrust the significance of relative position. Once the appendage buds appear, doubt as to identity is removed and a definite caudal progression of abdominal segmentation can be followed (embryo No. 9 on). (See General Discussion for further remarks.)

Following closely upon the initial demarcation of an abdominal segment, the mesodermal mass becomes detached from the neighboring mesoderm, first anteriorly, then posteriorly (fig. 38). This mass then divides medially into two lateral masses. Finally a cavity appears within each lateral mass, forming a coelomic sac with a wall consisting of a single layer of cells (figs. 37, 39). The cavity seems to arise as a simple fissure between the cells. There is evidence that the gnathal and thoracic mesoderm first becomes one-layered and that the dorsal wall of the coelomic sacs is derived from cells that shift mesad from the lateral border. The latter is suggested by appearances sometimes encountered in transverse sections (cf. fig. 39). (*Pteronarcys* thus resembles *Caurausius* (Wiesmann, in Leuzinger et al., 1926) in the formation of coelomic sacs. Roonwal (1937) describes the formation of gnathal,

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EXPLANATION OF FIGURE 2

The graph indicates the differentiation recognizable in each embryo and, by means of the heavy lines connecting the embryos, the course of its initial appearance. Further differentiation or retrogression of structures, after their initial appearance, is not indicated. The embryos are not drawn to scale; the extent of the tailpiece is arbitrarily represented and is not indicative of prospective significance. (In Nos. 8, 11, and 12, the degree of abdominal development is uncertain owing to unfavorable sectioning, hence no advance is shown. In No. 9, the protocormic appendages show a gradation in size, with the mandibles smallest and the three pairs of subequal legs largest.)

The table at the bottom is a summary, showing in which embryo a given differentiation is first apparent.

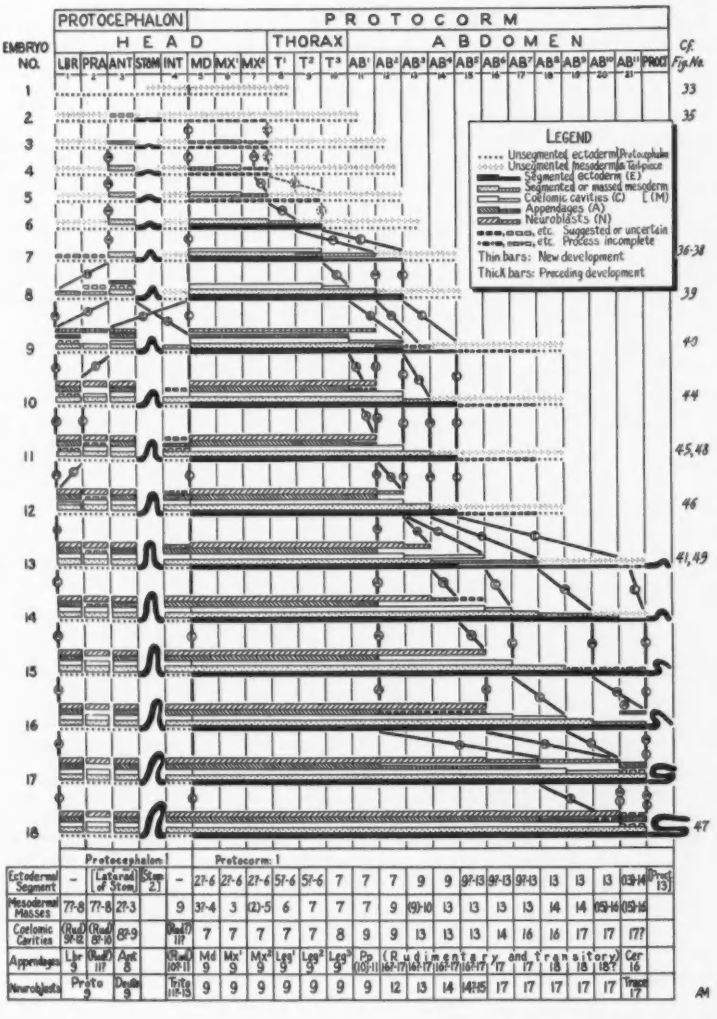

Fig. 2. Chart showing the sequence of morphological differentiation in the germ band of *Pteronarcys proteus*. (See text for critical remarks.) Based upon a study of twenty representative embryos (Nos. 6 and 10 stand for two embryos each); embryo No. 1 in stage II–III; Nos. 2–8 in stage IV; Nos. 9–15 in stage V; Nos. 16–18 in stage VI. For graph symbols, see legend; for other abbreviations, see p. 471.

thoracic, and first abdominal coelomic cavities in *Locusta* by the lateral edge of the mesoderm folding over dorso-medially; in the rest of the abdomen a horizontal fissure arises medially in a bilayered mass.) As the appendages develop in the mandibular to first abdominal segments, inclusive, the ventral portion of the corresponding coelomic sac extends into each (figs. 6, 40). In the abdomen short ventral extensions of the coelomic sacs indicate the presence of rudimentary and transitory appendages on segments 2 to 7. These, with the exception of the second and perhaps the third, are not evident externally and are distinguishable in cross sections only as ectodermal bulges flanking the developing nerve cord (stage VI). As the sides of abdominal segments 8 to 10 grow up around the lengthening proctodaeum, their coelomic sacs become vertical in extent, the tenth slanting caudad; 8 and 9 show ventral angles, but they are less marked than in the more anterior somites (fig. 47).

The proctodaeal invagination carries in with it a ventral enveloping layer of mesoderm which remains independent of the later-developing coelomic sacs of the caudal segments (8–10). The proctodaeal mesoderm probably belongs morphologically to the eleventh abdominal segment, or to a theoretical telson. At most only vague indications of eleventh abdominal coelomic cavities occur in the mass of mesoderm at the base of the cerci.

Anteriorly the mesoderm extends itself as a single thin layer of cells over the dorsal surface of the protocephalon, except for a marginal zone which is left bare (figs. 35, 36). It was not determined whether the mesoderm spreads forward as a complete sheet from the base of the protocephalon or goes around the stomodeal site and leaves a gap above it. At any rate, the gap is present in early stage IV, as indicated in figures 2 (embryo No. 2) and 35. The material studied gives no evidence of a forked protocephalic mesoderm; it is invariably closed around the front of the incipient stomodaeum. Before the antennal buds become evident, small masses of mesoderm form above their sites posterolaterad of the stomodaeum. Later these lie within the buds and each acquires a cavity which enlarges as the antenna grows. Postoral in early stages, the antennae become adoral and finally preoral (stage VII) as the protocephalic lobes turn up and the head develops. A mesodermal mass in front of the stomodaeum comes to occupy the labral rudiment and eventually shows a pair of very small cavities which may reflect a paired origin of this organ, although the latter seems to arise as a single medial evagination (figs. 35, 36, 45, 46). The left and right cavities are well separated and each is surrounded by a single layer of mesoderm cells. The mesoderm is bilobate but confluent medially. Another sign of doubleness of the labrum is the bilobate appearance of transections of its base during stage V (figs. 42, 43); this is lost in later development. The cavities disappear without enlarging before the mesoderm becomes mesenchymoid. As the stomodaeal invagination deepens in stage V, the mesoderm at each side forms a mass in which appears a definite trace of a cavity (figs. 44, 45). Although barely patent, its position is indicated by the encompassing arrangement of the neighboring mesodermal cells; this is apparent in at least five embryos and hence seems not to be merely fortuitous. Since their vestigial cavities are separate

from and anteromesad of the antennal coelomic cavities and posterolaterad of the labral cavities, it is possible to regard the small masses of mesoderm flanking the stomodaeum as rudimentary coelomic sacs homologous with the "preantennal coelomic sacs" of *Carausius* (Wiesmann, in Leuzinger et al, 1926).[7] They probably contribute to the stomodaeal musculature. A slight bulge of the ectoderm beneath each mesodermal mass (fig. 45) may represent a very rudimentary appendage, but it is indefinite at best and perhaps is not distinct from the swollen rim of the stomodaeum. The labral, preantennal, and antennal mesoderm is closely interconnected and invests the stomodaeum anteriorly and laterally. In the "intercalary" region behind the stomodaeum the mesoderm remains single-layered until the mandibular and other protocormic coelomic sacs and appendage buds are well developed (stage V). Small ectodermal projections are then apparent between the antennae and mandibles, near the lateral edges of the embryo (figs. 48, 49); these are interpreted as the evanescent appendages of the intercalary or tritocerebral somite. Associated with each of these is a small overlying mass of mesoderm, with no indication of a cavity other than a vague suggestion of a minute central fissure in one specimen. These mesodermal masses are evidently vestigial intercalary coelomic sacs. Unlike the medially-located rudiments in *Carausius*, they are widely separated and not directly connected with each other; they are close to, but distinct from, the mandibular coelomic sacs which lie behind them. The intercalary appendages are no longer apparent in stage VI and do not take part in the formation of the hypopharynx which arises in stages VII–VIII as a ventral projection of the consolidated gnathal sterna.

These observations on the protocephalic region, in the absence of detailed neurogenic studies, are insufficient to justify final conclusions concerning the segmentation of the head. It is possible to interpret them as suggesting that seven segments are involved—four protocephalic (including the intercalary) and three gnathal—as indicated in figure 2. This would agree with the views of Wiesmann (Leuzinger et al, 1926) who regards the antennal and rudimentary labral, preantennal, and intercalary coelomic sacs of the protocephalon in *Carausius* as evidence of segmentation. If this is true, a hypothetical acron must be postulated, as an unrecognizable part of the protocephalon that is homologous with the annelid prostomium. Roonwal (1937) found labral but no preantennal coeloms in *Locusta*, but also regards the head as composed of seven segments. (For other counts and discussions, see the reviews by Wiesmann and by Imms, 1937.) However, Snodgrass (1935, 1938) is inclined to regard these supposed evidences of preoral somites as secondary developments, the first true cephalic somite being the postoral tritocerebral (intercalary) segment. He presents lucid and credible arguments against a somitic interpretation of the preoral region and homologizes the entire protocephalon (exclusive of the intercalary region) of the insect embryo with the prostomium of Anne-

[7]The rudimentary cavities in *Pteronarcys* were erroneously interpreted as intercalary coeloms in the original unpublished thesis (Miller, 1938); confirmation of their anterior position and other observations herewith recorded invalidate this view.

lida, basing his view upon comparative studies of annelid and arthropod embryology and morphology, with especial regard to the nervous system and mesodermal development. It follows that, of the protocephalic appendages, only the intercalary pair is to be regarded as serially homologous with the protocormic appendages. The present observations on *Pteronarcys* shed no new light on the question. True, the protocephalic mesodermal cavities are directly comparable in number and position to those of other insects, and this added evidence of constancy ostensibly supports the view that the protocephalon is made up of fused somites, supposedly represented by these more or less rudimentary coelomic sacs. However, it is also possible to regard the cavities as homologous secondary structures and to attribute their constant position to similar mechanical or physiological conditions in the embryos of the several species. Since the facts so far known can be interpreted from either point of view, further discussion at this time would serve no useful purpose. The listing accorded the protocephalic region in the chart (fig. 2) simply indicates the topographical arrangement of its constituents, which may or may not have segmental significance.

DEVELOPMENT OF THE APPENDAGES: THE PLEUROPODIA

Only the development of the pleuropodial appendages will be here considered in detail. The suggestions of preantennae and the rudimentary intercalary appendages disappear before stage VII. All the other paired appendages, which function after eclosion, attain their definitive form after they have become segmented (mandibles excepted) and the second maxillae have fused to form the labium of the chewing mouthparts. (See synopsis of development and plate I in Miller, 1939.) Antennae and cerci are the last to show segmentation; their segments increase in number during postembryonic life by intercalary additions at the base of the flagellum in the antennae and at the base of the cerci. Gonopods or genital appendages do not develop during embryonic life, and no trace of them is apparent during the early postembryonic instars. The thoracic and abdominal tracheal gills develop in the egg during stage X. They are not, of course, primary appendages but simple, fingerlike, hollow outgrowths of the hypodermis. They number sixteen in the first postembryonic instar, each a single filament, and are arranged in eight pairs with the members of each pair widely separated. Each thoracic sternum bears two aligned pairs, one near the anterior border, the other between the coxae. The first and second abdominal sterna bear one pair each, with the gills also in anteroposterior alignment but further from the median line than the thoracic gills. The vestigial pleuropodial orifices lie mesad of the first abdominal gills. In other words, the abdominal gills lie laterad of the true appendages while the thoracic gills lie mesad of them. The gill filaments increase in number during later instars by new branches arising basally; in the older naiads the gills thus become large tufts.[8]

[8]Air does not appear in the closed tracheal system until the second instar. This is perhaps correlated with increased muscular activity, as Sikes and Wigglesworth (1931) suggest for other insects. The first instar of *Pteronarcys* is inactive, takes no food, and subsists on the yolk remaining in the mid-gut, while the second instar begins to forage for algae immediately after ecdysis.

The *pleuropodia*, paired appendages of the first abdominal segment homodynamous with the legs, first appear in stage V as ventro-caudally projecting limb buds (fig. 6). They are smaller than the leg buds, but like them become lined with a ventral extension of the corresponding coelomic sac (fig. 47). During subsequent development, as shown in figures 7 to 13, these buds are modified into transitory ectodermal glands which degenerate before the insect hatches. They are recognizable in the first postembryonic instar only as a pair of widely separated, nodular thickenings in the cuticula of the first abdominal sternum, one on either side just laterad of the ganglion and mesad of the gill. Each thickening is a cicatrix representing the occluded orifice of the pre-existent gland.

In the embryo, the apical ectodermal cells of each pleuropodial bud become distinguished by somewhat larger and more vesicular nuclei. These cells are invaginated by overgrowth of the surrounding ectoderm (stage VI, figs. 7, 8) and form a spherical gland which eventually comes to lie imbedded in the ventral wall of the segment. As the gland develops, the nuclei assume a peripheral position, forming one or two rows in cross-sections of the gland. Earlier than this, during stage VII, the cytoplasm of the invaginated cells becomes longitudinally striate. It also acquires a definite outer boundary which stains sharply with light green, suggestive of a striated border (fig. 9), but too thin for determination of its true nature even with the oil immersion objective. The border disappears with further development as the striate cytoplasm begins to grow out into the fluid (page 473) that bathes the embryo after blastokinesis (stage VIII, fig. 10). These apparently fibrillar outgrowths finally form a large, mushroom-like or penicillate tuft projecting from the gland. The outer zone of this tuft shows basophilic concentrations which probably are cross-sections of the splayed fibrillar bundles. This is the condition of both glands in stage IX (fig. 11) and presumably represents the period of principal, or at least final, physiological activity (see below). Thereafter the entire pleuropodium degenerates. The fully developed body of the gland measures about 40 μ in diameter and 44 μ high, but may be compressed by surrounding structures. The two glands are about 120 μ apart, separated by the first abdominal ganglion.

During stage IX secretion of the definitive cuticula is begun by the hypodermis, while the pleuropodial tuft is still projecting through it. This leaves a small pore in the cuticula which is still patent in stage X after the tuft has disappeared, and nothing remains internally of the gland except a few degenerate nuclei (fig. 12). The pore is almost occluded by a yellowish or horn-colored substance that shows a strong affinity for light green and for iron hematoxylin. After hatching, this material forms a compact plug lying in a depression in the cuticula that is formed by the hypodermis which has closed above the site (fig. 13). A vestige of a canal still persists in the plug, the material of which may be the shrunken residue of the tuft that disappeared early in stage X (about five months before normal hatching).

Slifer (1937) has demonstrated that the pleuropodial glands in the grasshopper are the source of a hatching enzyme which digests the serosal cuticle, and it seems probable that they serve a similar function in *Pteronarcys*. In this species, thinning and erosion of the serosal

cuticle (p. 472) become apparent in stage X, after the pleuropodia have passed their peak of development and have begun to degenerate. The weakening of the cuticle may be caused by enzymatic products liberated by the pleuropodial glands, though the visible effects of their action is somewhat delayed. The eroded depressions in the cuticle (fig. 14) appear to be negative images of the cuticular surface of the embryo: perhaps pressure at the point of contact abets the digestive action of the peri-embryonic fluid, or it may merely make local impressions on the membrane which is possibly softened throughout, before the rugulosities of the body cuticula appear. It is an open question, of course, whether the pleuropodia possess additional functions during their existence (see page 460).

The pleuropodial glands of *Pteronarcys* are of the invaginate type, while those of the grasshopper are evaginate (Roonwal, 1937; Slifer, 1938b). The extruded fibrillar tuft of the *Pteronarcys* type may be regarded as a device to provide an increased secretory surface (more strictly, an "outlet" surface) which in the grasshopper is attained by lobulation of the evaginate gland itself. In the latter no fibrillae are extruded and the cells are simply bounded outwardly by a striated border. Pleuropodia strikingly similar to those of *Pteronarcys* occur in the aquatic bugs *Belostoma* and *Ranatra*, as comparison with the photographs by Hussey (1926) shows. Hussey found mention of pleuropodia in the literature for 46 species in 32 families of 14 insect orders. Of these the Homoptera and Hemiptera (and also Lepidoptera—Hirschler, 1928) possess the invaginate type; many Coleoptera have intermediate invaginate types, while others have evaginate types similar to the Orthoptera; in other orders they are either rudimentary or available descriptions were fragmentary. In the invaginate tufted type Wheeler (1890) regarded the extruded threads as a secretion product, while Hussey interpreted them as clusters of cell tips; the latter is probably the sounder view. The parasitic, ovoviviparous polyctenid bug *Hesperoctenes* has highly developed invaginate pleuropodia, the tufts of which Hagan (1931) describes as completely surrounding the embryo, secreting a cuticle, and perhaps acting as a kind of placental organ. The same author has recently described still more bizarre evaginate pleuropodia in a tropical roach (Hagan, 1939). Since the pleuropodia assume such diversified forms in different insects, they undoubtedly can serve various purposes. Much still remains to be learned concerning these interesting organs, and correlation with habitat, structure, and development of the egg should prove enlightening.

ORIGIN OF THE MID-GUT

The development of the alimentary canal will be described in detail in a separate paper. In view of the bearing it has on the germ-layer question, it should be mentioned here that the definitive mid-gut epithelium in *Pteronarcys*—as far as determined to date—evidently arises solely from a posterior mid-gut rudiment. The latter is composed of cells that at first form the circumferential walls of the subapical part of the proctodaeum and that become differentiated only after the proctodaeum is well formed. (Similar cells give rise to the three Malpighian tubules.) The apical closure of the proctodaeum ruptures, and

the enlarged mid-gut rudiment cells are everted to form a discoid, unilayered plate. The cells of this rudiment spread forward over the yolk-side of the ental membrane and increase mitotically (but not as proliferating bands) until they enclose the entire yolk as a squamous epithelium with widely spaced nuclei (see figure 1). The epithelial cells become cuboidal by the time hatching occurs, but their definitive columnar form is not attained until the first postembryonic ecdysis approaches. In the non-feeding first instar, the mid-gut is lined by a cellular membrane that must originate either from the mid-gut epithelium or from vitellophags; this is evacuated during the first molt and replaced by a true peritrophic membrane in the second instar. Most, if not all, the vitellophags degenerate before hatching occurs. For discussion, see the following section.

General Discussion

Remarks of general interest are here presented, supplementing the more detailed comparative notes given in the preceding sections.

The serosal cuticle is evidently a structure common to a number of insects, as already indicated (p. 438). It may be more prevalent in insect eggs than the paucity of references would lead one to believe, since it is probable that such enclosing membranes have been sometimes discarded and given but little attention by students of insect embryology. The tough serosal cuticle provides additional protection to the developing embryo and is particularly important in this regard if the chorion should break open, as it sometimes does (dorsally) in *Pteronarcys*, late in development, perhaps due to growth pressure within the egg. The grasshopper chorion also may crack when dry and leave the cuticle as the main protection (Slifer, 1937). As the egg of *Dystiscus* enlarges, "the chorion splits and falls away and the egg is enclosed only in the vitelline membrane and serosal cuticle" (Wigglesworth, 1939, p. 2, citing Blunck). The possibly homologous membrane in Collembola eggs is also especially important as a protective device, for Wheeler (1893) states that following its formation in *Anurida*, the egg enlarges "till the chorion and vitelline membrane are burst" and the cuticle alone remains intact.

The evident homology of the grumorium and grumulus of *Pteronarcys* with the hydropyle and its cells in the grasshopper egg (p. 439) raises interesting phylogenetic and physiological questions. What has been the direction and manner of modification of this structure as to morphology and function in different insect groups? Does water absorption occur only or mainly through this structure in aquatic as well as terrestrial eggs? The small size and convex form of the core of the grumorium in *Pteronarcys* would seem to militate against a hydropyle function here; perhaps the thin outer cuticle allows the passage of water anywhere through the egg surface. The question can be answered only by experimental means. *Pteronarcys* may illustrate the more primitive mode of genesis of this organ—the cuticular grumorium is perhaps merely an incidental by-product of a residual clump of serosal cells left behind when the germ disc invaginates. On the other hand, if the progenitors of stoneflies reverted to an aquatic habit after a specialized hydropyle had arisen in terrestrial eggs, the condition of the structure

may be degenerate in *Pteronarcys*. There is here need for detailed investigation of the comparative ontogeny of the structure and of the probable phylogenetic relations of the insects themselves. The ventral surface of the stonefly egg is evidently homologous with the posterior pole of the grasshopper egg (see Miller, 1939, p. 597); the respective positions of the grumulus (mid-ventral) in the former and the hydropyle cells (polar) in the latter also support this view, which may be extended to include some other insects having a polar grumulus. (See also remarks on page 431.)

The serosa itself is quite typical in its structure and position, as well as in its contraction during blastokinesis to form a dorsal organ and its final disintegration in the yolk. Blastokinesis is essentially like that common in the eggs of exopterygote insects (e. g., acridid Orthoptera, Isoptera, Odonata, Heteroptera, and Homoptera). In *Pteronarcys* it involves not only a forward movement of the embryo but also a rotation of 90 degrees on the embryo's longitudinal axis. The change in position is clearly correlated with the form of the egg and with the most economical utilization of the space available for growth. One might speculate whether the unexplained rotation of the embryo on the longitudinal axis that is observed in certain elongate eggs (e. g., *Melanoplus:* Slifer, 1932) could be a phylogenetic anachronism having its basis in evolution from progenitors that developed in subspherical eggs.

Amnion formation in *Pteronarcys* by invagination of the ventral plate (p. 442) is directly comparable to amnion formation in other insects by convergence of marginal folds or by the germ band sinking tail-first into the yolk (as in *Platycnemis* and *Tachycines*). The difference in appearance is due to its early and rather abrupt occurrence, while the embryonic rudiment is still discoid. Since the amniotic cells are at first just as thick as the cells of the incipient germ band, the embryo appears as a minute hollow sphere (cf. Miller, 1939, p. 598).

The subsequent caudal elongation of the *Pteronarcys* embryo is similar to that found in Isoptera and Orthoptera, and the caudal addition of segments (at least in the abdomen) is strongly annelid-like in character. The data at hand indicate only that the morphological differentiation center is anterior in position, probably as a natural result of the embryonic rudiment representing mainly cephalic material at the outset. The inner layer first appears at the caudal border of this original material; if inner layer cells are added from the ectoderm at the base of the protocephalon in subsequent development (see page 454), this area would be justly regarded as the morphological differentiation center. It remains undetermined whether or not a caudal shift occurs later, to the usual position of the center in the first thoracic segment (cf. Richards and Miller, 1937). The phylogenetic reason for the anterior position of the differentiation center may well be sought in those forms, like *Pteronarcys*, that originate from a rudiment that seems to be predominantly cephalic in its prospective significance. As far as our present knowledge goes, the character and sequence of initial segmentation in the anterior protocorm seems to differ among orthopteroid insects. According to Wiesmann (Leuzinger et al, 1926), the mesoderm in the phasmid *Carausius* divides directly into microsomites, apparently simultaneously in the head and thorax; while in the grass-

hopper *Locusta* (Roonwal, 1936) and the camel cricket *Tachycines* (Krause, 1938) three prosegments or macromeres, besides the protocephalon, are first formed in the mesoderm, to be later subdivided into definitive somites. However, in all these species, in other Orthoptera, and in Isoptera, abdominal segmentation progresses caudally as the germ band elongates, as it does in *Pteronarcys*. In *Tachycines* Krause says the first mesodermal division to appear is that between the second maxillary and prothoracic segments. However, the locus of initial inner-layer formation seems to vary and makes it difficult to recognize a definite morphological differentiation center in this regard—perhaps due to variation in the position of the embryo relative to a physiological differentiation center in the yolk. Krause, in his extended discussion, gives other evidences of a prothoracic differentiation center, but it seems to be less definite or dominant than in other insects studied from this point of view. He sets up a series of egg types (*Tachycines*, *Gryllus*, *Platycnemis*, *Chrysopa*, *Apis*) which show a gradual decrease in the importance of the cleavage center and in the growth of the segment-forming zone, concomitant with a gradual increase in the importance of the differentiation center and in the size of the initial embryonic rudiment. On the basis of the initial size and extent of caudal growth of the rudiment, *Pteronarcys* evidently precedes *Tachycines* in this series, and the suggested cephalic position of a differentiation center would, if confirmed, further support this arrangement. Both *Pteronarcys* and *Tachycines* in the caudal progression of segmentation recall annelid development, except that teloblasts are absent. In *Tachycines* a further difference lies in the sequence of early segmentation, while in *Pteronarcys* the possibility remains open that this difference is lacking or is less marked. The question also arises, however, whether an almost simultaneous differentiation of the more anterior protocormic segments can be correlated with the distinctive behavior of primary somites (simultaneous early differentiation) and secondary somites (added by caudal growth) in annelids and some arthropods other than insects (see Snodgrass, 1938). It is also of interest to note that, although there is in the stonefly no evidence of a limited subterminal zone of growth like that in annelids (Snodgrass, 1938), it is theoretically possible to regard the mesoderm as analogously caudal in origin. In both, the mesoderm originates in the currently caudal region, but the process is continuous in the annelid during elongation, while in the stonefly the initially segregated mesoderm seems to increase in extent by unlocalized intrinsic growth concurrent with the growth of the entire embryo that carries the prospective tail region backward.

Krause (1938) points out resemblances between the development of *Tachycines* and the endolarvae of Archannelida and Polychaeta and suggests they may indicate the phylogenetic origin of the caudal flexure which is so universal in immersed insect embryos. *Pteronarcys* also shows a typical caudal flexure. Here it is preceded by a broad arching of the abdominal region of the germ band that may be, ontogenetically, partly the result of the attachment of the caudal extremity to the mid-ventral serosa during elongation (see plate I, Miller, 1939). While this may lead mechanically to a caudal flexure, it is doubtful that this is its sole determinant. In later development (early dorsal closure of

caudal segments and efficient utilization of the space available in the egg), the caudal flexure probably does afford a mechanical advantage. There is reason to believe, however, that it also has a phylogenetic significance.

The number of segments developing from the protocorm in *Pteronarcys* is seventeen (three gnathal, three thoracic, eleven abdominal), the last of which may incorporate a theoretical telson. The coelomic anlagen arise primarily in association with the appendage buds, as in other mandibulate exopterygotes and in contrast to the Coleoptera, which have limb buds filled with compact mesoderm and the coelomic cavities limited to the laterodorsal parts of the germ band (see Wiesmann in Leuzinger et al, 1926). In addition to the seventeen protocormic segments, there are three pairs of coelomic cavities (two rudimentary) in the protocephalic region, viz., labral, preantennal, and antennal, and a pair of mesodermal cell masses in the intercalary region. Of these, only the intercalary masses may be of true somitic significance. No apical acron has been recognized as a real entity in the protocephalon of this species. The head may thus be regarded as containing either seven segments, or four segments and a non-somitic procephalic region. In this connection, the reader is referred to the authors cited on page 000.

The question of the germ layers in insects has been adequately and recently reviewed by Eastham (1930) and Roonwal (1937, 1939). The present author prefers not to add to the existing confusion of the problem by adopting a dogmatic and premature attitude but wishes merely to mention the possible position of *Pteronarcys* in this regard. Unlike many higher insects, this stonefly does not have the inner layer arising by so-called gastrular invagination. Instead, it evidently arises by a shift or proliferation (?) of cells upward from the outer layer, in a very limited region and without the formation of a groove, while the embryo is still very short (i. e., in the median dorsocaudal portion of the spheroid embryo). Subsequent increase, at least in the protocorm, seems to be independent of further additions from below. The inner layer seems to consist of mesoderm only and to include no endoderm, for there is no evidence that it contributes to the formation of the mid-gut epithelium. The status of the endoderm is, of course, the crux of the problem. Since the mid-gut epithelium, like the Malpighian tubules, seems to arise from cells that are at first an integral and subterminal part of the proctodaeal invagination (not arising merely as proliferations from its apex), the most direct, and perhaps most tenable interpretation is to regard it as of ectodermal origin. This would relegate representation of the true (primary) endoderm to the vitellophags and secondary nuclear aggregates (p. 462). (The yolk-cell layer of *Carausius*, the possible homologue of the secondary aggregates, is also regarded as primary endoderm by Leuzinger, 1926.) An alternative interpretation would apply to the mid-gut rudiment the concept of latent endodermal cells (Johannsen, 1929) or of "end-ectoderm" (Roonwal, 1939), formed during a delayed gastrulation phase. However, these views when applied to the stonefly appear suspiciously circumventive or hypertheoretical. Perhaps, after all, only the vitellophags may be justly homologized with the endoderm of other invertebrates, using the term "endoderm" in a strictly embryological sense, rather than

in a functional or anatomical sense (as it is when the mid-gut tissue is called endodermal by virtue of its definitive position). To extend the embryological concept of the term further, in forms refractory to its application, subjects the germ-layer theory to so severe a strain that it loses its essential characters if not its entire meaning. In our preoccupation with terms there is danger of losing sight of the true nature of living matter—its remarkable adaptability; adaptability that may invalidate our best-intentioned attempts to pigeon-hole its other manifestations. (Cf. discussion by Tiegs and Murray, 1938, p. 218–224.) The author's tentative view is that, on the whole, the evidence accumulating—especially from investigations of the more primitive insects (and these should carry more weight in a problem of this kind than more specialized forms, with their greatly condensed course of development)—seems to favor the vitellophag-endoderm theory. Conditions found in *Pteronarcys* certainly do not militate against that theory. The subject of mid-gut formation will receive more detailed consideration and elaboration in a later paper.

The phylogenetic significance of the ental membrane is also an open question, and speculation is inadvisable pending more definite knowledge of its ontogenetic origin and its occurrence in other insects. Its function of separating the yolk from the developing body cavity of the embryo and serving as a base for the spread of the mid-gut epithelium seems to mark it as an adaptive structure to contend with certain exigencies of development in an egg rich in yolk. Its early extra-coelomic position argues against viewing it in the light of a peritoneal or blood-vascular structure. What its ancestral homology may be and whether it has any more definitive role to play, e. g., in the formation of dorsal or ventral diaphragms, are important problems that must be left for the future.

Though predominantly orthopteroid in its embryological development, *Pteronarcys* also shows resemblances to the Heteroptera and Homoptera in the invaginate, tufted type of pleuropodia (p. 460); also, less specifically, in the embryonic cuticle and cephalic egg tooth (p. 447), and in the serosal cuticle and grumulus (p. 438).

SUMMARY

1. A typical serosa develops directly from the cells of the primary epithelium (blastoderm) that remain at the periphery of the egg. A small, mid-ventral clump of residual serosal cells (the "grumulus") is formed at the site of invagination of the germ disc and remains associated with the caudal end of the embryo during early growth, as a point of attachment. After blastokinesis, the serosa forms a typical dorsal organ and disintegrates in the yolk.

2. A thick serosal cuticle is secreted on the outside of the serosa, including a nodular "grumorium" under the grumulus. The cuticle is partly eroded before hatching occurs.

3. The amnion arises as the ventral wall of the spheroid embryo (with a central amniotic cavity) formed by invagination

of the germ disc. It becomes thinner as the embryo grows, is everted during blastokinesis, and finally is incorporated into the dorsal organ.

4. A thin "ental membrane," associated with distinctive cells, develops and covers the entire upper surface of the embryo, separating it from the yolk. It is attached to the marginal ectoderm, but its mode of origin is undetermined. During dorsal closure it is carried upward by the advancing body wall and encloses the yolk; it serves as a surface for the spread of cells that form the definitive mid-gut epithelium.

5. An embryonic cuticle and cephalic egg-tooth are secreted by the ectodermal epithelium, before the definitive cuticula is formed, and are lost during hatching.

6. The vitellophags are presumably all of the secondary type, most derived directly from the primary epithelium, but some from dissociation of "secondary nuclear aggregates" that arise in conjunction with the germ disc. "Yolk cleavage" occurs, and paracytes are formed in the early embryo.

7. The embryo developing from the spheroid rudiment first lies upon the ventral serosa. As it elongates, it arches upward in the middle and finally becomes fully immersed in the yolk, extending across the diameter of the egg. During blastokinesis (a mechanical necessity in this species) the embryo again attains a superficial position, but extends along the circumference of the egg with its ventral surface outermost and the yolk enclosed above it in the everted amnion. As the body wall grows dorsally, the embryo becomes coiled with its legs central and finally hatches by bursting the egg at the junction of floor and dome.

8. The inner layer, apparently representing mesoderm only, arises dorsocaudally in the spheroid embryo as a small group of median cells, by dorsal displacement and perhaps proliferation of cells from the outer (ectodermal) layer, without the formation of a "gastrular groove." Further additions from below in the stages immediately following, if they occur at all, are probably limited to the basal protocephalic region.

9. As the embryo elongates, protocephalon and protocorm differentiate. Segments first become clearly demarcated in the gnathal and thoracic regions; others are added posteriorly as the embryo lengthens, by successive differentiation from an unsegmented tail-piece. Labral, preantennal, and antennal pairs of mesodermal cavities appear in the protocephalon, and

three gnathal, three thoracic, and ten abdominal pairs of coelomic sacs in the protocorm; the rudimentary intercalary coelomic masses and the mesoderm of the eleventh abdominal segment show no distinct cavities. In the abdomen the first (pleuropodial) and eleventh (cercal) pairs of appendages are most distinct; the others are rudimentary and transitory, as are also the suggested preantennal and the minute intercalary appendages.

10. The pleuropodia are of the invaginate, tufted type found also in hemipteroid insects.

11. The definitive mid-gut epithelium seems to arise from a posterior rudiment that develops in the subapical walls of the proctodaeum.

12. These and related features of stonefly embryogeny are compared to those of other insects, and their general significance is discussed.

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ABBREVIATIONS USED IN PLATES AND TEXT FIGURES

(Capitalized abbreviations refer to text figure 2)

AB^1–AB^{11}, ab^1–ab^{11}, first to eleventh abdominal segments.
ag^2, secondary nuclear aggregate.
am, amnion.
amc, amniotic cavity.
an, anus.
ANT, ant, antenna.
br, brain.
c, core of grumorium.
Cer, cer, cercus (appendage of eleventh abdominal segment).
cf, cytoplasmic fragment.
$co.ab^1$–$co.ab^{10}$, first to tenth abdominal coelomic cavities.
co.ant, antennal coelom.
co.int, rudimentary intercalary coelomic sac.
co.lbr., labral coelom.
co.md, mandibular coelom.
$co.mx^1$, $co.mx^2$, first, second maxillary coelom.
co.pra, preantennal coelom.
$co.t^1$, $co.t^2$, $co.t^3$, first, second, third thoracic coelom.
cph, cephalad.
cut, definitive cuticula.
cyt, cytoplasmic connection.
Deuto, deutocerebrum.
do, dorsal organ.
dp, degeneration product (pycnotic nucleus).
ec, embryonic cuticle.
ect, ectoderm.
em, ental membrane.
emc, ental membrane cell.
et, egg-tooth.
exc, filiform excrescence.
fb, fat body.
fgng, frontal ganglion.
fib, fibrillae; protoplasmic processes of pleuropodium.
fp, foot-plate.
fv, fat vacuole (negative image of fat droplet).
g, globule.
gc, ganglion cells (region).
gl, gland; gland cells.
gng, ganglion.
$gng.ab^1$, first abdominal ganglion.
$gng.t^3$, third thoracic ganglion.
gr, grumulus.
grm, grumorium.
hyp, hypodermis.
inl, inner layer.
INT, intercalary segment.
int.ap, intercalary appendage.
l, leg; l^1, l^2, l^3, first, second, third leg.
LBR, lbr, labrum.
MD, mandibular segment.
md, mandible.
md.seg, mandibular segment.
mes, mesoderm.
mg.ep, mid-gut epithelium.
mgr, mid-gut rudiment.
mus, muscle.
MX^1, MX^2, first, second maxillary segment.
Mx^1, Mx^2, first, second maxillae.
nb, neuroblast.
nur, neuropile.
p, paracyte.
pcm, protocorm.
pcph, protocephalon.
pfl, peri-embryonic fluid.
plg, pleuropodial plug.
Pp, pp, pleuropodium (appendage of first abdominal segment).
PRA, preantennal region.
pra(?), suggestion of preantennal appendage.
PROCT, proct, proctodaeum or proctodaeal lumen.
Proto, proto, protocerebrum.
Rud, rudimentary.
sc, serosal cuticle.
sc^1, outer layer of serosal cuticle.
ser, serosa or serosal nucleus.
ser^1, degenerating serosal cells.
spl.mes, splanchnic mesoderm.
ss, shrinkage space.
STOM, stom, stomodaeum.
T^1, T^2, T^3, t^1, t^2, t^3, first, second, third thoracic segment.
tp, tail-piece.
Trito, tritocerebrum.
v, vitellophag.
vp, ventral plate (germ disc).
y, yolk or yolk body.

EXPLANATION OF PLATES

All drawings were made with the aid of a camera lucida. Magnifications on the printed page and the stains employed are stated in the explanation of the figures.

PLATE I

Vitellophags, Embryonic Membranes, and Pleuropodia of *Pteronarcys proteus* Newm.

EXPLANATION OF FIGURES

Fig. 3. Vitellophags: *a*, from stages I and II, showing varied appearance; *b*, apparently a secondary nuclear aggregate pulling apart (stage II); *c*, *d*, vitellophags with associated globules (stage VI). a, Feulgen; b, borax carmine; c, d, alum hematoxylin. All × 640.

Fig. 4. Surface view of definitive serosa, showing cell boundaries and nuclei. Alum hematoxylin. × 100.

Fig. 5. Vertical section of grumulus, with overlying embryo cut transversely through protocorm (stage III). Alum hematoxylin. × 435.

Fig. 6. Sagittal section of right pleuropodium (stage V), showing typical appendage bud. Feulgen and light green. × 465.

Fig. 7. Sagittal section of left pleuropodium (stage VI), showing hypodermis overgrowing glandular portion. Feulgen and light green. × 465.

Fig. 8. Sagittal section of right pleuropodium (stage VI), showing gland further invaginated. Alum hematoxylin. × 465.

Fig. 9. Sagittal section of right pleuropodium (stage VII), showing invaginate gland with striate cytoplasm, no longer appendicular. Feulgen and light green. × 465.

Fig. 10. Sagittal section of left pleuropodium (stage VIII), showing fibrillae beginning to grow out of gland. Alum hematoxylin. × 465.

Fig. 11. Sagittal section of left pleuropodium (stage IX), showing fully developed tuft. (Segment sectioned horizontally.) Alum hematoxylin. × 465.

Fig. 12. Vertical section of right pleuropodium (stage X), showing degeneration. (Segment sectioned transversely.) Alum hematoxylin. × 465.

Fig. 13. Vertical section through right pleuropodial cicatrix in first postembryonic instar, showing complete disappearance of gland. (Segment sectioned transversely.) Alum hematoxylin and eosin. × 465.

Fig. 14. Section of serosa and serosal cuticle (stage III). Borax carmine. × 640.

Fig. 15. Section of corroded serosal cuticle (stage X). Eosin. × 640.

Fig. 16. Sagittal section of dorsal organ (stage VIII). (Lower end of figure toward head of embryo.) Feulgen and light green. × 325.

Fig. 17 a-c. Early ental membrane cells from a stage-V embryo. The cross-hatched areas represent the dorsal surface of the germ-band. Feulgen and light green. × 945.

Fig. 18. Lateral portion of transection of abdomen of a stage-VII embryo, showing attachment of ental membrane to ectoderm. Feulgen and light green. × 435.

Fig. 19 a-c. Definitive ental membrane cells and associated membrane, from a stage-VII embryo. *a*, *b*, acid fuchsin; *c*, Feulgen and light green. × 945.

Fig. 20. Transection through abdomen of a stage-VII embryo, showing position of ental membrane. Feulgen and light green. × 295.

Fig. 21. Surface view of egg-tooth with its foot-plate. × 55.

Fig. 22. Portion of sagittal section of head of a stage-IX embryo, showing the egg-tooth and embryonic cuticle. (Muscles and blood cells omitted.) Iron hematoxylin. × 210.

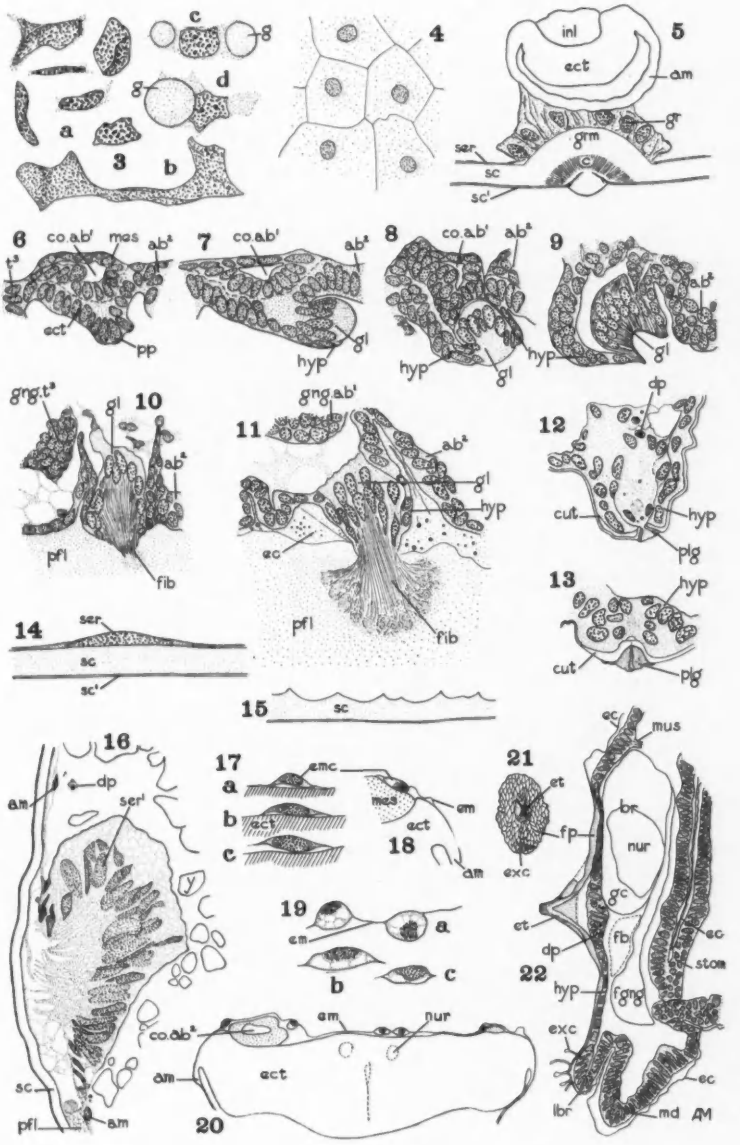
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PLATE II

Early Morphogenesis and Inner-layer Formation in *Pteronarcys proteus* Newm.

EXPLANATION OF FIGURES

Fig. 23. Ventral plate (germ disc) beginning to invaginate; vertical section. Thionin and orange G. × 420.

Fig. 24. Ventral plate completely invaginated, but embryo not yet consolidated; vertical section. Feulgen and light green. × 420.

Fig. 25. Early spheroid embryo (stage I); sagittal section. Borax carmine. × 420.

Fig. 26. Ovoid or pyriform embryo (stage I–II); sagittal section, slightly oblique. Feulgen and light green. × 420.

Fig. 27. Pyriform embryo (stage II); true sagittal section. Feulgen. × 420.

Figs. 28–29. Transections of slipper-shaped embryo (late stage II): 28, through base of protocephalon; 29, through protocorm. Feulgen. × 420.

Figs. 30–32. Transections of early protocephalic-lobe stage (III): 30, through protocephalon; 31, through intercalary region (transition from protocephalon to protocorm); 32, through protocorm. (Amniotic and most ectodermal nuclei omitted in 30 and 31.) Feulgen and light green. × 420.

Fig. 33. Mid-sagittal section of slipper-shaped or early protocephalic-lobe stage (II–III). Unless otherwise indicated, larger dark spots are mitotic figures, the smaller are paracytes. (Embryo No. 1, fig. 2.) Feulgen and light green. × 285.

Fig. 34. Vertical section of a stage–III egg aside from embryo, showing yolk-cleavage. Schaudinn's fixative; Feulgen and light green. × 41.

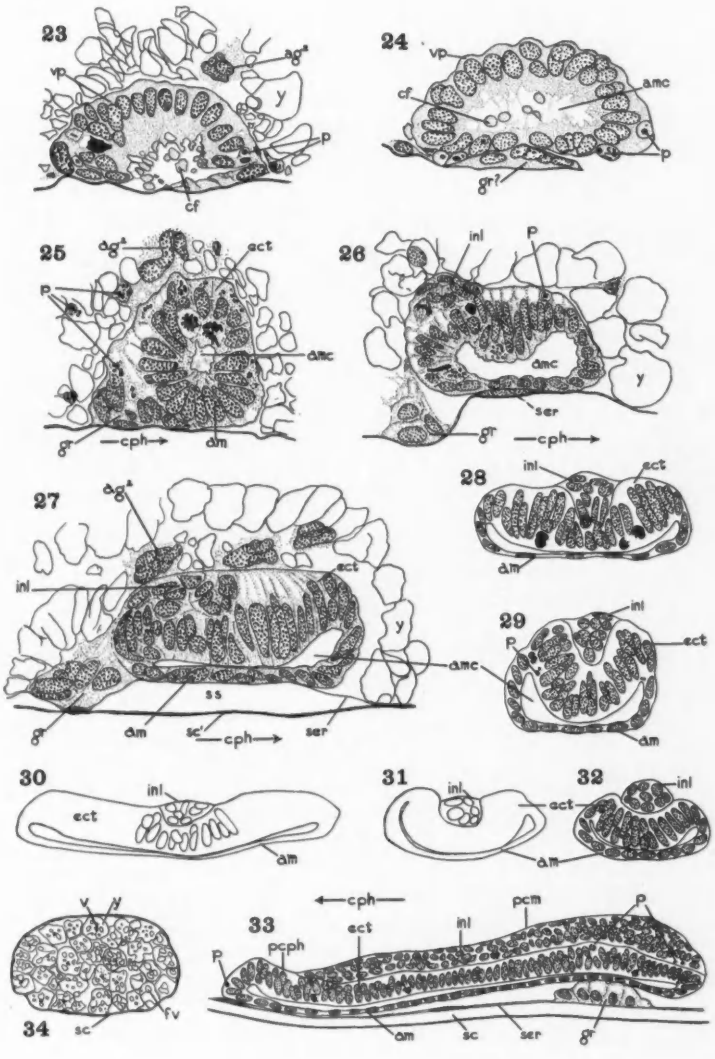
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Plate III

Segmentation and Formation of Coelomic Sacs in *Pteronarcys proteus* Newm.

EXPLANATION OF FIGURES

Fig. 35. Portion of mid-sagittal section of a stage–IV embryo, showing the incipient stomodaeum and protocephalic mesoderm. (Embryo No. 2, fig. 2). Feulgen and light green. × 415.

Fig. 36. Sagittal section of another stage IV embryo, along median line in protocephalon (before the artificial break shown) and to one side of the mid-line elsewhere; compiled from several sections. (Embryo No. 7, fig. 2). Feulgen and light green. × 140.

Fig. 37. Enlarged portion of fig. 36, showing incipient coelomic cavity in the first thoracic segment. × 415.

Fig. 38. Enlarged caudal portion of fig. 36, showing the unsegmented tail-piece. × 415.

Fig. 39. Transection through the first maxillary segment of another stage–IV embryo, showing formation of coelomic sacs. (Embryo No. 8, fig. 2.) Feulgen and light green. × 415.

Fig. 40. Portion of a sagittal section of a stage-V embryo, showing the coelomic sacs in the leg buds (latter marked "ect"). (Embryo No. 9, fig. 2.) Feulgen and light green. × 415.

Fig. 41. Sagittal section of caudal portion of a stage–V embryo, showing incipient proctodaeum and attachment to grumulus. (Embryo No. 13, fig. 2.) Alum hematoxylin. × 415.

Fig. 42. Transection of protocephalon of a stage–V embryo showing doubleness of base of labrum. (Same embryo as fig. 44, but a more anterior section.) × 140.

Fig. 43. Portion of frontal section of protocephalon of a stage–V embryo, showing the paired appearance of the labral mesoderm (stippled). Alum hematoxylin. × 140.

Fig. 44. Transection of protocephalon of a stage–V embryo, showing the rudimentary preantennal coelom. Section slightly oblique, with more posterior structures to the right (=left side of embryo). (Same embryo as fig. 42; No. 10, fig. 2.) Feulgen and light green. × 415.

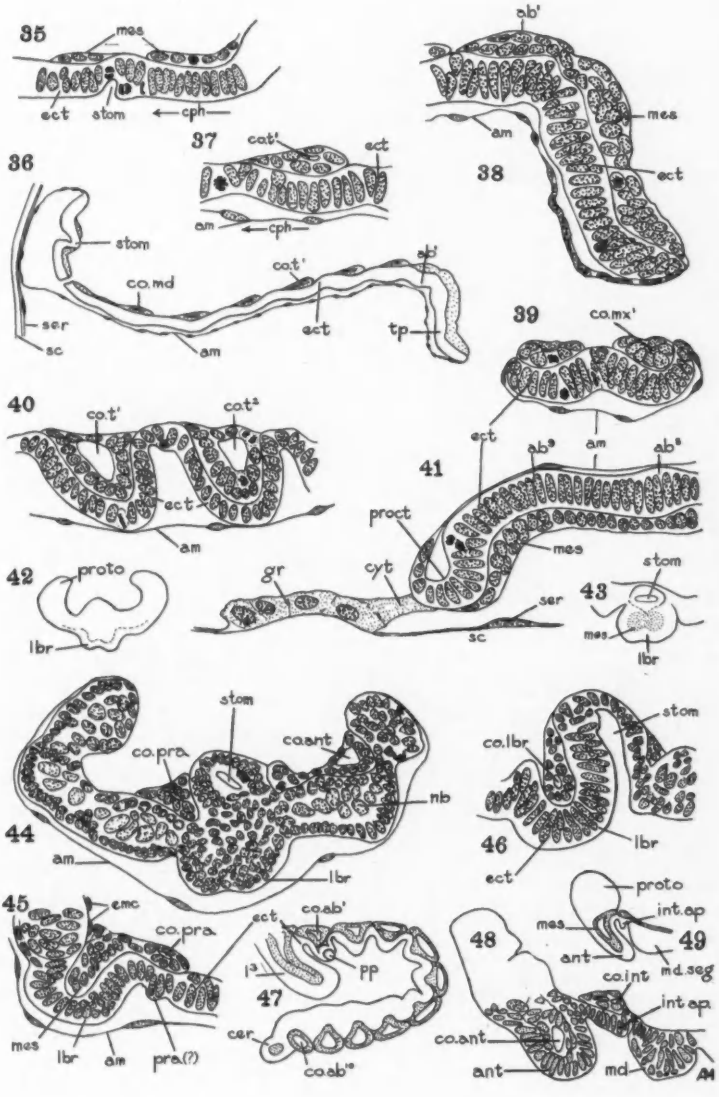
Fig. 45. Portion of sagittal section of a stage–V embryo to one side of stomodaeum, showing labral mesoderm and left preantennal coelom; the ectodermal protuberance below may be the preantennal appendage. (Embryo No. 11, fig. 2.) Feulgen and light green. × 415.

Fig. 46. Portion of a sagittal section of stage–V embryo, showing the labral coelomic cavity of the right side. (Embryo No. 12, fig. 2.) Feulgen and light green. × 415.

Fig. 47. Portion of a sagittal section, toward one side, of a stage–VI embryo, showing the abdominal coelomic sacs; compiled from several sections. (Embryo No. 18, fig. 2.) Alum hematoxylin and eosin. × 140.

Fig. 48. Anterior portion of another, more laterad, sagittal section of the embryo in fig. 45, showing the rudimentary intercalary coelomic sac and appendage of the right side. (Embryo No. 11, fig. 2.) × 355.

Fig. 49. Anterior portion of sagittal section of another stage–V embryo, showing the intercalary appendage. (Same embryo as fig. 41; No. 13, fig. 2.) Alum hematoxylin. × 140.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BOOK NOTICES

THE GREAT NATURALISTS EXPLORE SOUTH AMERICA, by PAUL RUSSELL CUTRIGHT. Pages xii and 340. Thirty-one plates and map, 9 x 5¾ inches. 1940. Published by THE MACMILLAN COMPANY, 60 Fifth Ave., New York. Price $3.50.

Doctor Cutright is Professor of Zoology at Beaver College, Jenkintown, Pennsylvania. He is from a family of naturalists. His father was a physician, one uncle was a botanist, another an ornithologist, another an entomologist. He is a brother of Dr. C. R. Cutright, entomologist, at the Ohio Agricultural Experiment Station, Wooster, Ohio.

Two evenings ago we sat down to give this volume the usual perfunctory reading (?). We closed the book last night at midnight after about eight hours of close attention. Ever since the reviewer had four years of the zoology and geography of South America under the tutelage of Professor Wm. J. Moenkhaus, just returned from two years as Assistant Director of the Museum at São Paulo, Brazil, and under Professor Carl H. Eigenmann, authority on South American fishes, his interest in that region has waxed rather than waned. However, such experiences do not wholly account for the long session with this book.

The exterior is an attractive linen binding. The illustrations are simple but specific. The frontispiece is an unusual portrait of Darwin as the young man who explored the coasts of South America. (One misses the beard, bulbous nose and wrinkles.) The text is divided into Part I, South America and the Naturalists, and Part II, which is a series of thirty parts, each on some specific animal or on some group of animals. Some titles run as follows: II. The Vampire Bat, III. Armadillos, IV. Sloths, V. Ant-eaters, VI. The Puma, VII. The Jaguar, X. The Tapir, XI. The Guanaco, XIV. The Monkeys, XVII. The Condor, XVIII. The Hoatzin, XIX. The Toucans, XX. The Hummingbirds, XXIII. Caimans and Crocodiles, XXIV. The Giant Boas, XXVIII. Electric Eels, XXIX. Jungle Pests, XXX. Insects as Food, XXXI. Butterflies.

Part I reviews the first period of natural history studies in South America. This was the work down to about 1910 and was the product of such great explorers as Alexander von Humbolt, Bonpland and Charles Waterton around the years 1799 to 1831; Charles Darwin, naturalist on H. M. S. Beagle, 1831–1836; Richard Schomburgk, 1841–1848; William H. Edwards, 1846; Alfred Russel Wallace and Henry W. Bates, 1848–1859; Richard Spruce, 1849–1869. These were fearless giants of exploration, men of remarkable literary, scientific and physical ability. Author Cutright figures that the average length of life of these men was eighty-one years. Humboldt reached ninety, Wallace eighty-nine and Waterton eighty-three.

Following this group was the remarkable W. H. Hudson, born in the Argentine, the explorer, as a youth, of the Pampas. At the age of twenty-seven he moved to England where he wrote four books on South American natural history and then turned to fiction with the volume "Green Mansions." Then came the equally gifted Everhard F. im Thurn, who later became an English colonial governor. To these can be added the names of Hesketh Prichard, and later Eugène André, whose volume, "A Naturalist in the Guianas," closes the heroic period of explorers.

By 1910 biological laboratories were being built in South America, some of these in the jungles themselves. Since then the basic study of South American biology has been taken over by these institutions. At present Brazil alone has 70 journals which publish biological articles.

So far, we have not touched upon the factors which give interest to the natural history of this region. Until very recent times geologically, South America was an area of three continental islands, (1) southeastern Brazil, (2) the Guianas and northern Brazil, and (3) the Cordillera. After each had developed, over long geological ages, its own rich fauna and flora, they coalesced and the Isthmus of Panama opened up a road for North American animals to enter. Four rich tropical faunas were thrown together. Bates took over 300 species of butterflies within walking distance of one village. In an equal area in the central United States 25 would be a good catch and our fauna is rich in species compared with

that of Europe. Add to this the extreme luxuriance of vegetation in the great Amazon and Orinoco Valleys where hot-house conditions prevail. Further, extreme taxonomic interest comes from the fact that through long geological periods of isolation the fauna and flora of South America is the second most primitive in the world. It stands between the extreme primitiveness of the biota of Australia and that of Southern Africa. Thus one has in tropical South America the richest of all lands in number of species, the land that all collectors hope to visit.

The feature of the work which we wish to call to the attention of all teachers of biology and librarians is the bibliography of six pages of works on South American natural history. These are not the many technical works on the subject but are in general books of travel, the narratives of explorers.—We must close.

—C. H. K.

BEITRÄGE ZUR BIOLOGIE UND BEKÄMPFUNG WICHTIGER ÖLERUCHTSCHÄDLINGE (Zur Biologie und Bekämpfung von *Ceutorrhynchus assimilis* Payk. und *Meligethes aeneus* Fbr.) by HUBERTUS A. VON WEISS. Monographien zur angewandten Entomologie. Nr. 14, pages 1–131, 54 illustrations, 6¾x10, paper, uncut. 1940. Published by PAUL PAREY, Hedemannstrasse 28–29, Berlin S. W. 11. Price, RM 9.

This monograph on the biology and control of two species of beetles attacking the seeds of cruciferous plants is not now of sufficient importance to American economic entomologists to justify an extensive review. In Germany, however, where these beetles reduce the domestic production of rapeseed oil, their control is an economic necessity.

In the first quarter of the monograph, the author gives a thorough account of the life history and biology of the Kohlschotenrüssler (cabbage shoot weevil). The remainder of the monograph deals with the control of this species and of the Rapsglanzkäfer (glossy rape beetle). The life history of the latter was well known and needed no investigation by the author.

We are indebted to Mr. J. A. Hyslop for the following information about the distribution and importance of these insects in the United States.

Ceutorrhynchus assimilis Payk. (cabbage shoot weevil) was reported in the State of Washington by W. W. Baker, Can. Ent. 68: 191. 1936, having been first discovered in May, 1935. In 1936 the insect was discovered in Oregon. It has been repeatedly reported since that time. Apparently some damage is being caused to the seeds of several cruciferous vegetables.

Meligethes aeneus (F.) (glossy rape beetle) has been known in the United States for many years and has been reported from coast to coast. It is very injurious to the seeds of cruciferous plants in Europe, but there are no records of such injury in the United States.—F. L. C.

THE CHEMISTRY AND TOXICOLOGY OF INSECTICIDES, by HAROLD H. SHEPARD. Pages i-iii and 1-383, 40 text figures, 8¼ x 10¾, paper, mimeographed, 1939. Published by BURGESS PUBLISHING CO., 426 So. Sixth St., Minneapolis, Minn. Price $4.00.

In 1927–28 C. H. Richardson, H. H. Shepard and this reviewer were working together in the Bureau of Entomology in Washington, D. C., on what was then a relatively new field of investigation, the toxicology of insecticides. In the order named we left the Bureau to learn more and to teach what we had learned to students in Iowa, Minnesota and Ohio. Knowledge of the chemistry and toxicology of insecticides has grown tremendously since our brief but happy period of association until today a substantial part of the *Journal of Economic Entomology* is devoted to the publication of papers in this field. A complete published inventory of the chemistry and toxicology of insecticides has been needed for some years. Until recently we had only the excellent but from our point of view incomplete book by Hubert Martin, "The Scientific Principles of Plant Protection." Last year appeared a German compendium of the desired

information,—a part of the all-inclusive work entitled "Handbuch der Pflanzenkrankheiten," issued by O. Appel. Now, thanks to Dr. Shepard, we have exactly what we want.

If one wants to know something about the composition or constitution of insecticides now in use or proposed for use, methods of chemical or biological assay of insecticides, effect of biological or environmental factors on their toxicity to insects or other organisms, etc., the answers, if known, are to be found in this book. In general, this book covers all information on insecticides that has been obtained in the laboratory. It deals therefore with the science of insecticides and not with the art of chemical control of insects. The student will not learn how to control an insect infestation by reading this book, but if he knows its contents and can serve as an apprentice in chemical control, he will better understand what he is doing and should be able to adapt his materials and methods to new situations. In research on the development of new insecticides or improvement of present insecticides this book will be most helpful.

Dr. Shepard is well known for his work on the toxicology of fumigants against stored product insects. Consequently the chapter on insect fumigants is outstanding. However, it is not out of proportion in length to other chapters in the book. Each chapter or each section of a chapter is concluded with a good bibliography. Scattered through the book are 40 text figures, most of them graphs taken from the literature to illustrate certain points that the author wished to drive home. Numerical data are given in 97 tables. Of special value are those tables that bring together chemical, physical or toxicological data for comparative purposes; e. g., Table 27 on median lethal doses of stomach poisons and Table 87 on median lethal concentrations of fumigants. As Table 5, Bliss' probits appear in a book for the first time. Useful conversion tables and tables of weights and measures are given in an appendix. The index appears to be adequate.

It ill becomes a man who was not able even to start an inventory of his special field to criticize the work of Dr. Shepard who successfully accomplished the task. Fortunately there is little to criticize and much to praise. Without special training on the chemical side, Dr. Shepard has nevertheless done a competent job. He has combed the English literature thoroughly and has not neglected patents nor the literature in other languages. His presentation is impersonal, for he rarely comments on the work of others or makes suggestions for further research. Frequently he uses quotations from the literature. As it stands now, the book is remarkably free from errors, typographical or otherwise. It is the kind of book that every teacher of a specialized technical subject ought to prepare for use of his students,—but few do. Such a book need not be a carefully finished product, for it should undergo frequent revision. If printed publication should become desirable, we hope that Dr. Shepard can find time to polish the book. It needs more condensation, more logical arrangement, and more subheads than it now has. We stand in awe of Dr. Shepard's accomplishments and are most grateful to him for making his work available to us and to our students.—F. L. C.

YOU AND HEREDITY, by AMARAM SCHEINFELD assisted in the genetic sections by MORTON D. SCHWEITZER. 434 pages, 117 illustrations and tables, 1939. Size 6x8.7 inches. For sale by FREDERICK A. STOKES CO., New York. Price $3.00.

The reviewer's wife asked for some simple and interesting work on heredity and eugenics: for a book which she could recommend to graduate girl students and other friends who might be interested, yet who were not familiar enough with the terms that ornament biology to enjoy the usual college text on the subject. The question was passed on to Professor Laurence H. Snyder, himself the author of a widely used text, just revised. Doctor Snyder's immediate answer was "You and Heredity." The above question and its answer, almost better than any review that might be given, define the present book and its usefulness to an enquiring world.

The author is a magazine writer who tried to use his own ideas on heredity in the plot of a novel, which manuscript had to be discarded when he found his own concepts in error. He then spent several years in the study of heredity, pub-

lished various popular articles on the subject and finally the present volume. The personal acknowledgments for checks and advice on various chapters read as a who's-who of genetics and allied sciences. He has been meticulous in this check by competent authorities. The author is also an artist, an illustrator of merit. This ability shows in his diagrams all through the volume.

The forty-three chapters have very brief titles and some are very catchy. We quote a few: II. Life begins at zero; V. Myths of mating; VIII. Boy or girl? IX. Super chain-gangs; XVI. What will your child look like? XVIII. Duplicated humans; XIX. The Dionnes; XXII. For men only; XXVI. The twilight sexes; XXIX. Achievement: Birth or luck; XXXV. Enter the villain; XL. The giddy stork; XLII. The program for tomorrow.

The volume is interestingly written, is strikingly illustrated and has been checked chapter after chapter by experts. It has been written by one who knows what interests the public and by one who has been willing to take the time necessary to produce a sound book. We are more than willing to recommend it to the wife, her students and her friends.—C. H. K.

THE SPIDER BOOK, by JOHN H. COMSTOCK, Revised and Edited by W. J. Gertsch, Ph.D. Pages xi+729, 770 text figs. 1940. Published by DOUBLEDAY, DORAN AND COMPANY, Inc., 75 Franklin St., Garden City, N. Y. Price $6.00.

From his position as associate curator of spiders in the American Museum of Natural History, Dr. Gertsch's competence to undertake the revision of The Spider Book and the adequacy of his resources for the work must be evident even to those who have no personal knowledge of his contributions to the study of the Arachnida. The result is a fine renewal of a valuable book, recognizable still as The Spider Book of Comstock, but with the advantage of modernization in essential details of taxonomy.

The Spider Book has never been adequate for the taxonomist who wants to pursue his species to the bitter end. Rather it has made available the general system of Arachnid classification with specific characteristics of a limited number of examples in the various genera, together with interesting accounts of the habits of these strange animals. Dr. Gertsch states frankly in his preface that he has left the book much as he found it. One can only agree with his statement: "Inasmuch as The Spider Book was intended as a popular introduction, it has seemed inexpedient to incorporate into the book controversial arrangement, debatable nomenclature, or radical departures from the present standard."

Changes have been introduced only in the taxonomic portions of the book. These show evidence of careful treatment in line with the conservative point of view expressed above. A check of the illustrations shows almost no change. Whether this is only another result of conservative treatment or a limitation that the reviser would not have chosen for himself, examination of the book does not disclose. Illustrations are of tremendous value in the taxonomy of arthropods, but perhaps additions of this kind would have detracted from the essential quality of the original work. In any case prospective experts will find abundant technical literature to help them, and here a bibliography including almost thirty new titles will be a useful guide, although it is still limited to works cited in the text.

The new edition creates the general impression that here an old friend is again brought into print—ably rejuvenated and in an attractive new cover, but not too much changed to be the same old and valued friend.—A. W. L.

REVISTA DEL INSTITUTO DE SALUBRIDAD Y ENFERMEDADES TROPICALES, Vol. I, No. 1, pp. 1-128, November, 1939. Published quarterly by the BIBLIOTECA DEL INSTITUTO DE SALUBRIDAD Y ENFERMEDADES TROPICALES, Mexico, D. F., México. Annual subscription price $3.00 American, 6 "dolares" Mexican.

We welcome a new American biological journal, the Review of the Institute of Health and Tropical Diseases of Mexico. This recently organized institute comprises seven laboratories, in seven branches of tropical medicine and a public

clinic. That which is of interest to our readers is the Laboratorio de Entomologia of which Dr. Luis Vargas, a graduate of Johns Hopkins University, is Director. On March 18, 1939, the Institute was dedicated by a ceremony presided over by the Private Secretary of the President, Señor Agustin Leñero. The Departments of the Government, the Diplomatic Corps and scientific institutions were represented. By invitation Professor Robert Hegner and Professor Reginald Hewitt of Johns Hopkins were present and during the following days advised on various scientific problems facing the scientific staff of the Institute.

The Revista carries six articles, all of which are on biological problems connected with public health. Three are in the field of entomology: one on infection carried by reduviids, by Luis Mazzotti; one on the chaetotaxy of larvae of Anopheles by Luis Vargas and a second by the same author on recent records of mosquitoes in Mexico.

The Revista is well printed except for its illustrations which are largely dim half-tones. The ANNALS once received some half-tones made in Mexico City. The metal was nailed on the warped blocks by small carpet tacks. The metal etchings had to be remounted and tuned up before they could be used in our accurately adjusted American presses. Apparently the Revista starts out with the handicap of poor technical help in the commercial engraving and printing plants. When we remember that the first book printed in the Western Hemisphere was published in Mexico City, we wonder that Mexican pride tolerates such work by engraving companies.

Our knowledge of Spanish fades badly at critical passages and has some static but we have read far enough to be able to transmit to our readers the invitation to American scientific men to visit and make use of the facilities of the Instituto. The ANNALS wishes the Revista success.—C. H. K.

PROBLEMS OF LAKE BIOLOGY, by nine author-experts, edited by F. R. MOULTON. Pages 142, 45 text figs. Size 7½ x 10½. 1939. Published for American Association for the Advancement of Science by THE SCIENCE PRESS PRINTING CO., Lancaster, Penn. Price $1.75.

This volume publishes a symposium on lake biology which was sponsored by the rather recently organized Limnological Society of America. Curiously enough, the introductory pages do not state when and where the symposium was given further than that it was given at a meeting of the Association.

Problems of Lake Biology is another book which on first inspection did not appear interesting and was shelved for several months until conscience (?) came to its rescue. We believe that any biologist who still retains a broad interest in biological problems beyond the confines of his specialty will consider it interesting. This interest arises from several factors. The lake is a microcosm, a complete little world or organism of its own. All lakes have a limited life of a youth, middle life and old age. The reader's spirit rises to the reassuring facts that he is dealing with a limited problem whose boundaries are within his comprehension and mastery. It is a psychological reaction to the matter to be read, just the opposite to that of attempting to master a volume on the expanding universe or on any other centrifugally organized subject. At the end of the latter type of essay the reader is still looking out over unexplained distances extending from the subject matter in all directions. The first type of reading feeds the reader's ego. Mastery is within his reach. The latter belittles one's ego and defeats it. To summarize our own essay: Problems of Lake Biology is an interesting, readable book.

The nine contributions and nine authors are as follows: "Some physical and chemical factors in the metabolism of lakes," by D. S. Rawson, University of Saskatchewan; "The utilization of solar energy by aquatic organisms," by George L. Clark, Harvard University; "Distribution of bacteria in lakes," by Arthur T. Henrici, University of Minnesota; "Some relationships of phytoplankton to limnology and aquatic biology," by G. W. Prescott, Albion College; "Zooplankton in relation to the metabolism of lakes," by Willis L. Tressler, University of Buffalo; "The microscopic fauna of the sandy beaches," by Robert W. Pennak, University of Colorado; "Rooted aquatic plants and their relation to the limnology of fresh-water lakes," by L. R. Wilson, Coe College; "Role of bottom

fauna in the productivity of lakes," by Frank E. Eggleton; "The position of fish and other higher animals in the economy of lakes," by F. E. J. Fry, University of Toronto.

Few persons are conscious of the vast and densely populated world of micro-organisms in which we live until a doctor mentions flu germs as he presents his bill or until he mentions Pneumococcus type three to the widow. In sand from the bottom of certain lakes, say a handfull, ten cubic centimeters, have been found 4,000,000 Bacteria, 8,000 Protozoa, 400 Rotatoria, 40 Copepoda and 20 Tardigrada. The soil of damp land is equally rich. It is a commonplace to count 2,000 insects on an area of one square yard. The non-biologist lives in a thinly populated world occupied by a few macro-organisms, large trees, many flowers, some weeds, a few cats, dogs and robins. In the middle distance are cows, horses, frogs and sheep, while farther away are elephants, whales, tigers, etc. Unfortunately, while we see the thin population of macro-plants and macro-animals we are actually immersed in a vast and densely populated world of micro-organisms. The plants and animals visible to man are the exceptional.

It is the kind and density of the micro-populations of lakes that control the value of lakes to man. The populations of micro-organisms are the substrata on which develop the organisms large enough to be of value to man. Because of the limited nature of lake populations in humidity, space and temperature, these inter-relationships can be more effectively studied with present methods than can the less definitely bounded land populations. Hence one of the values of limnology as against land biology.

The present volume gives us some vivid views into these various relationships of populations to each other and to physical factors. The book is a basic summary of the subject. We know of few books where so much interesting information in well bound form can be had for $1.75.—C. H. K.

THE BIONOMICS OF ENTOMOPHAGOUS INSECTS, Part II, by WALTER VALENTINE BALDUF. 384 pages, 228 figures, size 8½ x 11¼ inches. 1939. Published and planographed by JOHN S. SWIFT CO., INC., Saint Louis, Mo. Price, cloth bound, $7.50.

This is the second number of the series of volumes on entomophagous insects planned by Professor Balduf. Volume one treated Coleoptera with similar food habits. We always admire anyone who has determination enough to write extensive works. From the "Acknowledgments" we find that the author has had financial help from the Bache Fund and from the research board of the graduate school of the University of Illinois. He has had a graduate student to help in abstracting and much help from Mrs. Balduf who has redrawn illustrations, typed manuscript and without doubt has fed courage into the mind of the author.

The present volume covers Lepidoptera, pp. 1–101, Trichoptera, pp. 102–186, Mecoptera, pp. 187–213, and Neuroptera, pp. 214–455. It is a review and thoroughly documented key to the literature. In general it follows in each group from the simpler (more expected) habits up through various stages to some of the most unexpected types of feeding.

Among entomophagous insects he recognizes three types, cannibals, predators and parasites. Then he adds to these a fourth group that bite and kill but do not eat their prey, the *homophonous* insects which thus practice *homophony* or plain murder; example, the corn ear worm when crowded. The most aberrant group appear to be some of the Lycaenid butterflies whose larvae emit a fluid loved by ants. The latter carry the caterpillars to their nests where the young butterflies live on ant larvae. The loving nurse ants appear to be fascinated by the glandular exudates of the caterpillars. Thus, even in ant society some lady ants have their price. Pages 95–101 are given to a review of the rise of entomophagy in the moths and butterflies which is one feature which makes the volume valuable. However, it throws loops in the average entomologist's vocabulary; to-wit: "How may the coccidophagy of the predacious amyrmecophilous homopterophags have originated?"

In the section on Trichoptera we have the best short review of general biology and habits of caddis flies in the English language. This is the one great group of rather large insects of which we know so little.

Because of the highly specialized nature of the habits of the various Mecoptera and Neuroptera the sections on these review the many novel adaptations of structure and habit distinguishing their families. These are the scattered tips of branches of the philogenetic tree of a great Mesozoic fauna of which only the highly specialized forms remain.

We wish to say one thing for the publisher. The reproduction is by the offset process, ignorantly termed mimeograph, but which the trade calls by various other trade names. This process is being gradually refined until only the experienced can tell that its product is not from set type. Even the paper used is of normal weight and not the thick bulky stock that had to be used in the early stages of the development of the process.

It is hoped that Professor Balduf can continue with this series. It is proving to be one of the most useful works in the hands of the student of the general biology and evolution of insects. Painstaking reviews done by experienced entomologists are about the most generally useful type of literature we possess.—C. H. K.

THE COLLECTED LETTERS OF ANTONI VAN LEEUWENHOECK. Edited, Illustrated and Annotated by a Committee of Dutch Scientists. In 20 volumes, large quarto with many plates and illustrations. Published by N. V. Swets & Zeitlinger, Bookdealers and Publishers, Keizersgracht 471, Amsterdam, Holland. Price, unbound, per vol., 19 guilders; canvas, 21.50 guilders; de lux edition, in 25 vols., 50 guilders per volume.

The above monumental work is in course of publication. The individual letters will be reproduced on one page and a translation into English on the facing page. This is the correspondence addressed to the Royal Society of London, to Huygens, Leibnitz, Magliabechi and others which stands more or less as Leeuwenhoek's publication of his discoveries with the microscope. He wrote no extended treatises but made many microscopes, and was constantly writing letters on his discoveries in that world of detail below human vision. He was one of the early students of the Protozoa and other microorganisms that could be found in a drop of stagnant water.

We only hope on this the sixth day of the attack on Holland that the present unpleasantness in that area will not destroy the extensive publishing and book trade of the Dutch cities. It certainly cannot help them. And what about the great Jewish book firms that emigrated from Germany to Holland to escape Nazi restraints?—C. H. K.

FORM AND CAUSALITY IN EARLY DEVELOPMENT, by ALBERT M. DALCQ. Pages vii and 197, 64 figs. Size 5½ x 8¾ inches. 1939. Published by CAMBRIDGE UNIVERSITY PRESS, Bentley House, Euston Road, London N. W. 1. Price 12s 6d. The Macmillan Co., 60 Fifth Ave., New York City. Price $3.50.

The author is Professor of Human Anatomy and Embryology at the University of Brussels. The present small volume was written to give the beginner in embryology a review volume with the general well established aspects of dynamic embryology in outline, rather than a detailed review with many complications such as those recently published by Spemann, Paul Weiss and others. While this volume deals with changing forces, its concepts are easily within the comprehension of those students whose daily work has to be expressed in terms of a concrete morphology. The author recognizes the two distinct methods of thought, one in terms of objects, the other in terms of forces, and has succeeded in giving those of us whose mental habit is one of thinking in terms of objects, a fairly understandable "picture" (?) of a science of forces. This ability in fitting the language to the subject is expressed even in the title. For about fifty years we have labored under a title, "Experimental Embryology." which expresses only method and does not fit the philosophy of the subject matter. Dalcq recognizes a distinct biological science and attempts to outline its field and operating forces.

Chapter headings are as follows: I. The recent embryological movement; II. An outline of Organogenesis; III. The kinematic aspect of embryogenic processes; IV. A comparative study of presumptive territories; V. The role of

induction; VI. Regional organization after cleavage; VII. Organization of the vertebrate egg before and during cleavage; VIII. The organization of the prochordate germ; IX. Field and gradient in the sea-urchin egg; X. Regulation in some other eggs.

Dalcq (p. 84) believes that his theory of the interaction (in the chordate embryo) of the yolk gradient and the dorso-ventral field provide us with the solution of development. That solution must fulfill the following requirements: (1) to remain close to the objective structure of the recently fertilized egg; (2) to reveal the functional sequence from that initial structure to the earliest morphogenetic events; (3) to explain the shape of the presumptive areas, the course of their boundaries and the orientation of the primitive segments; (4) to account for the results of experiments including those of the grafts of organizers; (5) to give an interpretation of determination; (6) to show the meaning of the power of specific assimilatory induction exhibited by the organs of the embryo.

Professor Dalcq pits the distribution of chemical and physical forces within the yolk (the yolk gradient) against the strains (forces) in the dorso-ventral field, i. e., between the dorsal animal pole and the ventral vegetal pole (chordate egg) as the interaction which controls development. He also emphasizes a powerful cortical factor associated with the blastoderm. The last idea agrees with philosophy of the organization of the cell recently reviewed in a volume by Just. Apparently Dalcq has given us principles that are more general and broader in application than are those of a mosaic of forces which have appeared as explanations in the majority of earlier writings on morphogenesis. He fits the "induction" of Spemann and "field" theories of Paul Weiss into this picture. He goes back farther and states that to understand the forces of embryonic development we must understand the forces that build the fertilized egg.

To the reviewer this is the most satisfactory volume of several we have read recently on the misnamed science of "experimental embryology." It is satisfactory to a general biologist or a beginner who is unfamiliar with the current controversies on the subject. Its logical language, built on a vocabulary using many concrete terms and its numerous explanatory diagrams, give us a volume understandable by one unfamiliar (through lack of use) with the language of students dealing with the interaction of centers of force, fields of force and gradients. We recommend it to those entomologists who wish to broaden a personal knowledge of biology.

It deals with the chordate egg and not the arthropod egg which shows major differences in development.—C. H. K.

DIE BRUTFÜRSORGE—UND BRUTPFLEGEINSTINKTE DER KAFER, by H. v. LENGERKEN. Pages VI and 285, 188 text figs. Size 6 x 8.5 inches. Published by the AKADEMISCHE VERLAGSGESELLSCHAFT M. B. H., Leipzig, Germany. Price, paper bound, RM 17.80, cloth, RM 19.60 (=$8.25).

Professor Doctor von Lengerken is a full professor of zoology at the University of Berlin. His research during the past twenty years has been on the habits of beetles. Some of his publications have been in co-authorship with the great zoologist, Richard Heymons, of the Berlin Zoologisches Institut. The author states in the introduction, "The present work is an experiment. It presents the essence of our present knowledge of provision for and the nursing of the young by the Coleoptera. This is the first of a series of volumes which it is planned to publish under the general title Ergebnisse der Insektenbiologie."

It is elaborately worked out under various subheads without the usual use of chapters. The major divisions are as follows: Protection of the egg; Provision of food; Provision of protection of the egg as well as protection and food for the larvae; Care of the larvae; Brood parasitism, and Psychological considerations. The last two occupy a total of one and a half pages.

The volume is a striking publication. The first thing which attracts the reader are the numerous brilliantly done illustrations, many of which are diagrams of nests and burrows. Others are series of diagrams showing how a beetle cuts and rolls a leaf, how a larva develops and forms its burrow within a dung ball. They are the clear, simplified kind of illustration that will be copied and recopied in entomological literature for years to come.

Apparently the earliest and simplest type of care for the young by beetles was that found in some Carabids (Carabus) where the mother merely laid eggs in a hole in the ground. This matter of care develops through the group up to such high forms as the scarabaeids where the dung beetles bury food balls for the future young and guard them until the young mature. A parallel habit obtains among the silphids. Between these extremes lie all those forms which dig galleries in timber, cut and roll leaves, build mud capsules for eggs, etc.

This most interesting volume should be read by all entomologists. It is an excellent work by a world authority on the subject. But it costs $8.25! A neighboring country which may soon become a province of Greater Germany publishes books of this size and amount of illustrations for from one to two dollars, cloth bound. We are publishing such in the United States for much less than five dollars. Greater Germany may become a very expensive luxury in the book trade.

During intellectual black-outs of mental and spiritual depression we sometimes wonder if we do not prefer good books to the glories of a world-enveloping Germany. But such verboten thoughts may be in grievous error. However, we like books and lots of them!—C. H. K.

LES PROGRÈS RÉCENTS DE L'EMBRYOLOGIE EXPERIMENTALE, by MAURICE CAULLERY. Pages 1–236, 395 text figs. 1939. Size 5 x 7.5 inches. Published by FLAMMARION, 26 rue Racine, Paris. Price, paper cover, Fr. 28.80 or 60 cents.

This is one of the review works on modern science published by Flammarion under the general title "Bibliothèque de Philosophie Scientifique." On the covers of this volume are listed about eighty titles of similar import in all branches of science. Among the authors listed are Nobel Prize winners and others of the great names in French science. The library includes works from leaders in other countries. We notice the name of Einstein, also "La Menace des Insectes," by L. O. Howard. We can recall no better or more reasonably priced set of books that might be very useful to one desiring to activate his reading knowledge of scientific French. This is not to be confused with a somewhat similar set of scientific works under the title "Encyclopedie Scientifique," published by Doin, Paris, an equally useful set. Price lists of both series and the books themselves can be obtained from Lechevalier, 12 rue de Tournon, Paris VI, France.

The First Part of the present volume, "Morphogenesis studied by observation of normal development," contains Chap. I. Initial Phases of the Development of the Egg, and Chap. II. Study of Normal Development by Application of Color-marks. The second chapter reviews the powerful technique invented by Vogt (1925) for staining spots on the living egg by applied bits of stained agar jelly. This technique permits the direct study of the translation of parts during development. It gave us our present knowledge of the formation of parts over the period of gastrulation and the formation of the major embryonic parts.

The Second Part, Chaps. III to the end (Chap. XIII) reviews the experimental work and theories of the many leaders in this subject which as a key to the forces of life has been at the center of biological discussion since the Renaissance. Chapter III reviews the mosaic theory by His, germinal localization of Chabry and Roux; the work of Driesch, etc.; Chapter IV. Merogony; V. Recent work on egg of the sea-urchin; VI. Morphogenesis in Amphibia (Spemann); VII. Induction; VIII. Analysis of induction (Mangold's work); IX. Special cases of induction; X. Mechanism and factors of induction; XI. Induction in non-aquatic vertebrates; XII. Insects (Hegner, Reith, Geigy, Seidel, Schnetter, Krause, etc.); XIII. The contributions of experimental embryology to teratogenesis.

This volume will be of use to any one at all interested in reviewing experimental embryology. It reviews the subject just enough from the historical point of view to tie the various developments into a logical time sequence. It is in a simple, direct language with ample (395) illustrations to clarify the descriptive passages. At the price of 60 cents for the paper bound edition one could hardly think of a better investment. The Bibliothèque de Philosophie Scientifique is full of just such bargains in biological literature.—C. H. K.

DOCTOR A. K. MORDWILKO